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GEOLOGY AND VERTEBRATE PALEONTOLOGY OF THE EARLY PLIOCENE SITE OF KANAPOI, NORTHERN KENYA

EDITED BY JOHN M. HARRIS AND MEAVE G. LEAKEY

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GEOLOGY AND VERTEBRATE PALEONTOLOGY OF THE EARLY PLIOCENE SITE OF KANAPOI, NORTHERN KENYA

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INTRODUCTION

JOHN M. HARRIS[1] AND MEAVE G. LEAKEY[2]

The site of Kanapoi lies to the southwest of Lake Turkana in northern Kenya (Fig. 1). Vertebrate fossils were recovered from Kanapoi in the 1960s by Harvard University expeditions and in the 1990s by National Museums of Kenya expeditions. The assemblage of vertebrate fossils from Kanapoi is both prolific and diverse and, because of its depositional context of fluviatile and deltaic sediments that accumulated during a major lacustrine phase, exemplifies a time interval that is otherwise not well represented in the Lake Turkana Basin. Kanapoi has yielded one of the few well-dated early Pliocene assemblages from sub-Saharan Africa but hitherto only the hominins, proboscideans, perissodactyls, and suids recovered from this locality have received more than cursory treatment. The four papers presented in this contribution document the geologic context and diversity of the Kanapoi fossil vertebrate biota.

HISTORICAL CONTEXT

The Lake Turkana Basin (formerly the Lake Rudolf Basin) traverses the western Kenya–Ethiopia border and has been an important source of Neogene terrestrial vertebrate fossils since the early part of the twentieth century (Coppens and Howell, 1983) (Fig. 1). In 1888, Count Samuel Teleki von Szék and Ludwig Ritter von Höhnel were the first European explorers to reach the lake (Höhnel, 1938), which they named Lake Rudolf after Crown Prince Rudolf of Austria-Hungary (1859–89). The subsequent French expedition of Bourg de Bozas (1902–03) recovered vertebrate fossils from Plio–Pleistocene exposures in the lower Omo Valley (Haug, 1912; Joleaud, 1920a, 1920b, 1928, 1930, 1933; Boulenger, 1920). This discovery prompted the Mission Scientifique de l'Omo (1932–33), which further documented the geology and paleontology of the area to the north of the Omo Delta (Arambourg, 1935, 1943, 1947). Allied military forces occupied southern Ethiopia during World War II; vertebrate fossils collected during the occupation were forwarded to the Coryndon Museum in Nairobi (now the National Museums of Kenya) and in 1942 L.S.B. Leakey (honorary curator of the Coryndon Museum) sent his Kenyan staff to collect from the southern Ethiopian Omo deposits (Leakey, 1943). Political unrest in both Kenya and Ethiopia after the end of the Second World War precluded further fieldwork in the area for more than a decade.

In the mid-1960s, L.H. Robbins investigated the terminal Pleistocene and Holocene archaeology of the southwestern portion of the Lake Turkana Basin (Robbins, 1967, 1972). Robbins let it be known that the region also contained somewhat older fossils and, in 1966, Bryan Patterson initiated a series of Harvard University expeditions to the region between the lower Kerio and Turkwell Rivers. Patterson's expeditions focused initially on the Kanapoi region (1966–67) and subsequently on Lothagam (1967–72). Assemblages from the two localities shed much light on the late Miocene–early Pliocene vertebrate biota of sub-Saharan Africa and provided the basis for monographic revisions of elephantids (Maglio, 1973), perissodactyls (Hooijer and Patterson, 1972; Hooijer and Maglio, 1974), and suids (Cooke and Ewer, 1972). The Patterson expeditions recovered few primate fossils but documented a hominid mandible from Lothagam (Patterson et al., 1970; Leakey and Walker, 2003) and a hominin humerus from Kanapoi (Patterson and Howells, 1967; Ward et al., 2001).

In 1967, a joint French, American, and Kenyan expedition (International Omo Research Expedition) resumed exploration of Plio–Pleistocene exposures in the lower Omo Valley. In 1968, the Kenyan contingent withdrew from the IORE to prospect the northeast shore of Lake Rudolf. The East Rudolf Research Project became the Koobi Fora Research Project when the Government of Kenya changed the name of the lake to Lake Turkana in 1975. The International Omo Research Expeditions (1967–76) and Koobi Fora Research Project (1968–78) recovered a great wealth of Plio–Pleistocene vertebrate fossils, including important new hominin material. Monographic treatment of material from the Omo Shungura sequence was published in the *Cahiers de Paléontologie* series edited by Y. Coppens and F. C. Howell (e.g., Eisenmann, 1985; Gentry, 1985; Eck and Jablonsky, 1987). That from Koobi Fora was published in the KFRP monograph series of Clarendon Press (Leakey and Leakey, 1978; Harris, 1983, 1991; Wood, 1994; Isaac, 1997).

During the 1980s, National Museums of Kenya expeditions under the leadership of Richard Leakey explored the sedimentary exposures on the west side of Lake Turkana (Harris et al., 1988a, 1988b). Small but significant Plio–Pleistocene vertebrate assemblages included the first cranium of *Australopithecus aethiopicus* (Walker et al., 1986) and a relatively complete skeleton of *Homo ergaster* (Brown et al., 1985; Walker and Leakey, 1993).

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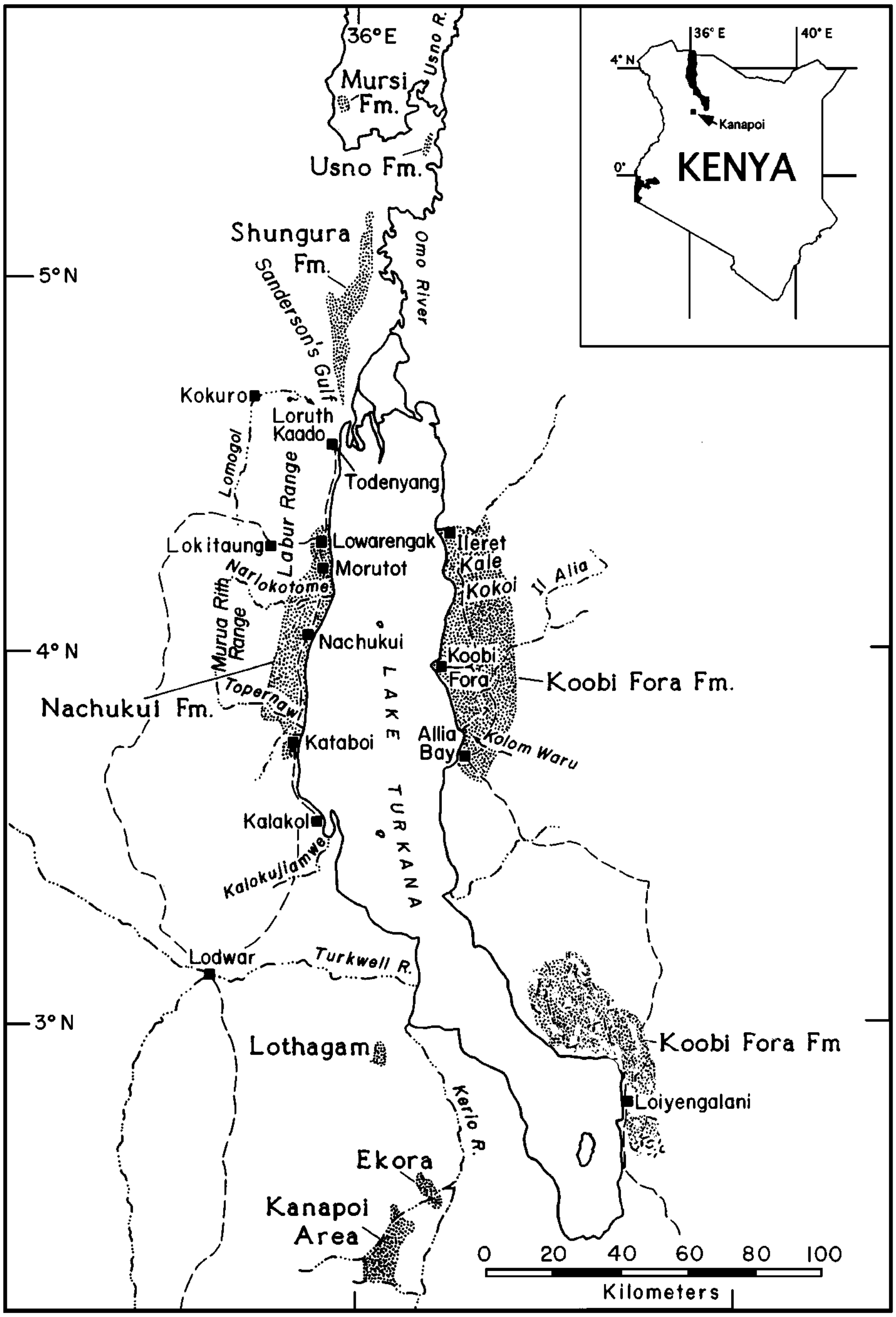

Figure 1 Map of late Miocene through Pleistocene fossiliferous localities in the Lake Turkana Basin (after Harris et al., 1988b)

During the 1990s, National Museums of Kenya expeditions, now under the leadership of Meave Leakey, concentrated on the southwest portion of the Lake Turkana Basin, discovering new localities (Ward et al., 1999) as well as revisiting Lothagam and Kanapoi. Lothagam was reworked from 1989 to 1993 and monographic treatment of the biota has now been published (Leakey and Harris, 2003). The Kanapoi locality was reprospected from 1993 to 1997 (Leakey et al., 1995, 1998). Hominin material recovered by the National Museums of Kenya expeditions has been described in detail (Ward et al., 2001); other recently recovered vertebrate species and their geologic setting provide the topic of this contribution.

GEOLOGICAL CONTEXT

The Lake Turkana Basin dates back to the early Pliocene. The present lake is sited in a closed basin that is fed year-round from the north by the Omo River, whose source is in the Ethiopian highlands and seasonally from the southwest by the Turkwel and Kerio Rivers and by other smaller ephemeral rivers. Paleogeographic reconstructions by Brown and Feibel (1991) indicate that, for much of the Pliocene, the Omo River flowed through the basin and directly into the Indian Ocean but occasional tectonic activity disrupted the outflow and resulted in short-lived temporary lakes. After about 1.9 Ma, the history of the region is still not clear. It is possible that the river no longer exited through the southeastern part of the basin, yet mollusks flourished until at least 1.7 Ma ago, implying that waters of the lake had not become as alkaline as they are at present. Indeed, mollusk-packed sands are reasonably common until at least 1.3 Ma ago (Harris et al., 1988a), so the basin may have remained open until this time either at the southern end, or alternatively, the lake may have occasionally overflowed to the northwest through Sanderson's Gulf into the Nile catchment.The Plio–Pleistocene terrestrial and lacustrine strata from the northern half of the basin form part of the Omo Group (Brown and Feibel, 1986) and are represented by the Shungura, Mursi, and Usno Formations in the lower Omo Valley (de Heinzelin, 1983), the Koobi Fora Formation on the northeast side of the lake (Brown and Feibel, 1991), and the Nachukui Formation on the northwest side of the lake (Harris et al., 1988a). The Nachukui Formation extends to the southwest of the lake where, at Lothagam, it overlies the late Miocene Nawata Formation (Feibel, 2003a). Figure 2 lists the members of the Koobi Fora and Nachukui Formations in stratigraphic order.

The oldest paleolake recognized in the basin is referred to as the Lonyumun Lake. It is documented by the lacustrine sediments of the Lonyumun Member, which was defined as the basal unit of the Koobi Fora Formation (Brown and Feibel, 1991) but also forms the basal unit of the Nachukui Formation on the west side of the lake (Harris et al., 1988a). The Lonyumun Lake is represented in the southwest part of the basin by the upper Apak and Muruongori members of the Nachukui Formation (Feibel, 2003a). The fossiliferous strata from Kanapoi include a short-lived lacustrine episode that corresponds with the Lonyumun lacustrine interval. Feibel (2003b) interprets the fluvial sediments that enclose the lacustrine phase to have been deposited by the Kerio River and has named the sequence the Kanapoi Formation. The Pliocene strata of Kanapoi thus provide the oldest record of fluvial sediments deposited by the Kerio River and include a deltaic tongue extending into the Lonyumun Lake. They thereby complement the fluvial sediments of the Kaiyumung Member of the Nachukui Formation at the nearby locality of Lothagam that were evidently deposited by the Turkwel River (Feibel, 2003a).

PALEONTOLOGICAL CONTEXT

As exemplified at the nearby site of Lothagam (Leakey et al., 1996; Leakey and Harris, 2003), there was a drastic change in the terrestrial vertebrate biota of sub-Saharan Africa at the end of the Miocene due to faunal interchange between Africa and Eurasia, and coincident with the worldwide radiation of C_4 vegetation (Cerling et al., 1997). The Kanapoi biota, dated radiometrically between 4.17 and 4.07 Ma (Leakey et al., 1995, 1998) lacks the large mammalian genera characteristic of the late Miocene at Lothagam—such as the amphicyonid carnivorans, the elephantids *Stegotetrabelodon* Pettrochi, 1941 and *Primelephas* Maglio, 1970, the teleoceratine rhino *Brachypotherium* Roger, 1904, the giraffid *Palaeotragus* Gaudrey, 1861, and boselaphin bovids (Leakey and Harris, 2003). Instead, the Kanapoi fauna demonstrates the first post-Miocene radiation of endemic African carnivorans (Werdelin, 2003) and a suite of ungulate species that is less progressive than that characteristic of late Pliocene exposures in the Lake Turkana Basin (Harris et al., 2003). The Kanapoi fish assemblage (Stewart, 2003b) is similar to but less diverse than that from the temporally equivalent strata at Lothagam (Stewart, 2003a).

Partly because of the widespread nature of the Lonyumun Lake, fluvial sediments with vertebrate fossils representing that time interval are rare in the Lake Turkana Basin. Fossils from horizons immediately before and after the Lonyumun lacustrine interval at the nearby locality of Lothagam have been described recently (Leakey and Harris, 2003). A hominin-bearing vertebrate assemblage slightly younger than that from Kanapoi has been recovered from the Koobi Fora Formation in Allia Bay on the eastern shore of Lake Turkana but thus far only the hominins have been described in detail (Ward et al., 2001). A few suid teeth from the Mursi Formation, collected by the Kenyan contingent of the International Omo Research Expedition in 1967, suggests that the oldest formation in the Omo Group (de Heinzelin, 1983) is of broadly similar age to the Kanapoi Formation. There are several small assemblages that have been recovered from localities south of the Turkwel River (Eshua Kakurongori, Longarakak, Nakoret, Napudet, etc.) but these have yet to be fully prepared or studied in detail.

OVERVIEW

The four papers presented in this contribution treat different aspects of the geology and vertebrate paleontology of the northern Kenyan locality of Kan-

Nachukui Fm (WT)	**Nachukui Fm (LT)**	**Kanapoi Fm**	**Koobi Fora Fm**
Nariokotome Mb			Chari Mb
Natoo Mb			Okote Mb
Kaitio Mb	Kaitio Mb		KBS Mb
Kalachoro Mb	Kalachoro Mb		Burgi Mb
Lokalalei Mb			Tulu Bor Mb
Lomekwi Mb			Lokochot Mb
Kataboi Mb	Kaiyumung Mb	Upper fluvial interval	Moiti Mb
Lonyumun Mb	Muruongori Mb and Lothagam Basalt	Lacustrine interval	Lonyumun Mb
	Apak Mb	Lower fluvial interval	

Figure 2 Stratigraphic sequence of the formal and informal members of the Kanapoi Formation, the Koobi Fora Formation and the Nachukui Formation where exposed in West Turkana (WT) and Lothagam (LT); for correlative details, see Harris et al. (1988b: fig. 4) and Feibel (2003a, 2003b)

apoi. However, their appearance together in a single publication will provide a useful source of reference for this interesting site.

Feibel describes the stratigraphy and erects a new formation for the Kanapoi succession. The environmental setting recorded by the Kanapoi sedimentary sequence reflects a progression of fluvial and lacustrine systems that overwhelmed a volcanic landscape. He interprets the vertebrate-bearing fluvial sediments to have formed part of the Kerio River system as it entered the Lonyumun Lake just over 4 million years ago. The high degree of landscape heterogeneity and pronounced soil catenas of the Kanapoi setting are indicative of a great mosaic of habitats in the southwestern part of the Turkana Basin during the early Pliocene.

Stewart describes the nearly 3,000 fish elements recovered from lacustrine sediments at Kanapoi during the early 1990s. The Kanapoi fish fauna mainly comprises large piscivores and medium to large molluscivores. The paucity of herbivorous fish such as mormyroids, *Barbus* Cuvier and Cloquet, 1816, *Alestes*, and distichodids is a little unexpected. While *Barbus* Müller and Troschel, 1841, and large tilapiine cichlids are scarce in African fossil deposits prior to the Pleistocene (Stewart, 2001), the other groups are represented in the Lothagam succession and one would expect them to be present in the Pliocene lake. The Kanapoi assemblage has many similarities with that of the Muruongori Member from the Lothagam succession. However, differences in representation of alestid and tetraodontid species suggest either that the Kanapoi lacustrine phase correlates temporally more closely with the Apak Member in the Lothagam sequence or that the Kanapoi and Muruongori fish assemblages sample different habitats. Stewart interprets the Kanapoi lake to be well oxygenated and nonsaline; the scarcity of lungfish, bichirs and *Heterotis* Ruppell, 1829 all of which were well represented in the Nawata Formation at Lothagam, could signify an absence of well-vegetated backwaters or bays.

Harris, Leakey, and Cerling document the diversity of tetrapods (exclusive of carnivorans) that have been recovered from Kanapoi. The mammalian fauna provides a standard for the early Pliocene in East Africa, with the cercopithecid, elephantid, rhinocerotid, suid, giraffid, and bovid species providing a link between those from upper Miocene levels at Lothagam and those in late Pliocene assemblages from elsewhere in the Lake Turkana Basin. Even though the microfauna has yet to be studied in detail, the Kanapoi mammalian biota is already larger and more diverse than the preliminary report of mammals from the slightly older site of Aramis in Ethiopia or from the Nachukui Formation members at Lothagam. Kanapoi is the type locality for the oldest East African australopithecine species yet recognized, *Australopithecus anamensis* (Leakey et al., 1995), so the Kanapoi biota is of interest for the information it provides about environments in which early bipedal hominins lived. No taphonomic investigation has yet been undertaken at the Kanapoi locality but, as pointed out by Behrensmeyer (1991), broad-scaled paleoenvironmental reconstructions based on the presence of taxa are likely to be accurate despite the taphonomic history of the assemblage.

The paleosols from the Kanapoi succession suggest a suite of habitats similar to those currently found in the vicinity of the modern Omo Delta at the north end of Lake Turkana. On the basis of their modern counterparts, the Kanapoi herbivores suggest a relatively dry climate and a mixture of woodland and open grassland. However, ecological structure analysis (cf. Reed, 1999) suggests closed woodland, and thus is closer to the wooded habitat interpreted for the slightly older hominin *Ardipithecus ramidus* (White et al., 1994) from Aramis in Ethiopia (WoldeGabriel et al., 1994). An appendix by Winkler provides a brief preliminary report on the micromammals.

Werdelin describes the carnivoran component of the Kanapoi biota, which is larger and more diverse than those from most Pliocene localities in eastern Africa and provides a substantial addition to our knowledge of early Pliocene African Carnivora. It shares a number of species with the slightly older Langebaanweg (South Africa) and the slightly younger Laetoli (Tanzania), but the overall mixture of species is unique to Kanapoi. The late Miocene Nawata Formation at Lothagam has yielded a number of carnivorans that were evidently migrants from Eurasia. The carnivoran assemblage from Langebaanweg also includes a number of relict Miocene forms but that from Kanapoi includes only forms whose immediate forebears are found in Africa. Kanapoi, therefore, provides evidence for the first post-Miocene radiation of endemic African carnivorans.

SUMMARY

The locality of Kanapoi is significant in that it has yielded an early Pliocene assemblage that includes representatives of the earliest East African species of *Australopithecus* Dart, 1925, and the vertebrate biota has the potential for providing a detailed picture of the environments exploited by early bipedal hominins. The assemblage is derived from fluvial and lacustrine sediments that are tightly constrained between tephra dated at 4.17 and 4.07 Ma. Paleosols in the sequence indicate the presence of terrestrial habitats that are today found at the north of Lake Turkana in the vicinity of the Omo Delta. In particular, they indicate the presence of a significant quantity of grass, given that the proportion of soil carbonate derived from C_4 plants varies from 25% to 40% in the paleosols associated with terrestrial fossils (Wynn, 2000).

Much of the terrestrial vertebrate assemblage was collected via surface prospecting and no detailed taphonomical investigations have yet been undertaken. Nevertheless, preliminary investigation of the mammalian fossils provides support for the environmental interpretations derived from the paleosols. Grazing mammals outnumber browsing forms by nearly two to one in terms of numbers of species and by three to one in terms of numbers of specimens. The microfauna has yet to be studied in detail, but initial investigation of some rodent species suggests they represent dry and open habitats (see Appendix in Harris et al., 2003). However, ecological structure analysis of the kind advocated by Reed (1997) suggests that the Kanapoi assemblage may instead be indicative of closed woodland as represented at Lothagam by the Kaiyumung Member of the Nachukui Formation or in the lower Omo Valley by Member B of the Shungura Formation. This apparent conflict of interpretation has yet to be resolved but may also be indicative that the habitats present in the region during the initial formation of the Turkana Basin may not be directly comparable with the modern habitats now characteristic of eastern Africa.

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STRATIGRAPHY AND DEPOSITIONAL SETTING OF THE PLIOCENE KANAPOI FORMATION, LOWER KERIO VALLEY, KENYA

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ABSTRACT. The Pliocene sedimentary sequence at Kanapoi is attributed to the Kanapoi Formation, newly defined here. The formation consists of three sedimentary intervals, a lower fluvial sequence, a lacustrine phase, and an upper fluvial sequence. The entire formation is strongly influenced by paleotopography developed on the underlying Mio–Pliocene basalts, with a landscape of rounded hills and up to 40 m in local relief. The lower fluvial interval is dominated by conglomerates, sandstones, and pedogenically modified mudstones. Two altered pumiceous tephra occur within this interval. A sharp contact marks the transition to fully lacustrine conditions. This interval is characterized by laminated claystones and siltstones, lenticular sand bodies, and abundant ostracods, mollusks, and carbonized plant remains. A single vitric tephra, the Kanapoi Tuff, occurs within this interval. A return to fluvial conditions is recorded first by upward fining cycles reflecting a meandering river system. This is succeeded by deeply incised conglomerates and sands of a braidplain, capped by the Kalokwanya Basalt. The Kanapoi Formation is richly fossiliferous, and has yielded the type specimen as well as much of the hypodigm of *Australopithecus anamensis*. Vertebrate fossils derive primarily from two depositional settings within the formation: vertic floodplain paleosols and deltaic sand bodies. These reflect successional stages in the development of a major tributary system in the Turkana Basin during the early Pliocene.

INTRODUCTION

The Pliocene sedimentary sequence at Kanapoi presents a complex record of fluvial and lacustrine strata deposited over a landscape of considerable local relief (up to 40 m) on Mio–Pliocene volcanics. Early fluvial systems accumulated predominantly overbank mudstones, with a well-developed soil overprint, associated with lenticular sands and gravels. A lacustrine phase, the Lonyumun Lake, in the middle of the sequence is marked by laminated claystones and molluskan bioherms, with thick deltaic sand bodies. Following local infilling of the lake, a fluvial regime is again represented. The top of the sedimentary interval is dominated by a thick and deeply incised conglomeratic unit that accumulated prior to capping of the entire sequence by the Kalokwanya Basalt.

Vertebrate fossils are found throughout the sedimentary sequence, being particularly abundant in the deltaic sand bodies, but are also found in paleosols of the lower and upper fluvial sequences. Fossil invertebrates are common in the lacustrine facies, though the quality of preservation tends to be poor. Lacustrine mudstones preserve abundant plant impressions and carbonized remains at several levels.

Isotopic age determinations on materials from Kanapoi by I. McDougall of the Australia National University (Leakey et al., 1995, 1998) established a precise chronostratigraphy for the sequence. The major phase of deposition is constrained to fall between 4.17 and 4.07 Ma, and the capping Kalokwanya Basalt is placed at 3.4 Ma. The Kanapoi deposits reflect an early stage of accumulation within the developing Plio–Pleistocene Turkana Basin.

The geological investigations reported here were conducted over eight visits to Kanapoi between 1992 and 1996. Field mapping and 21 stratigraphic sections are the basis for a formal definition of the Kanapoi Formation presented here. Analysis of depositional environments, postdepositional modification, and sedimentary architecture are the basis for a reconstruction of the environmental setting for the rich Kanapoi fossil assemblage.

BACKGROUND

The sedimentary strata around Kanapoi were first described by Patterson (1966). He recognized many of the important features of the local geology. The interval he described was predominantly lacustrine in character and comprises the middle unit in the sequence described here. No formal stratigraphic terminology or subdivision of the strata was proposed, although a section measuring 175 ft. (53.3 m) is mentioned. The first report of a hominid fossil from Kanapoi by Patterson and Howells (1967) included a few additional observations on the geology of the sequence.

Patterson et al. (1970) discussed the Kanapoi fauna, and used the term 'Kanapoi Formation' for the sequence, but provided no descriptions, sections, or type locality. The most detailed geological work conducted prior to the 1990s was Powers'

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(1980) investigation of strata of the Lower Kerio Valley. He provided sections and descriptions of the sedimentary strata at Kanapoi, as well as an interpretation of depositional environments and post-depositional modification. Most of the early discussion of Kanapoi centered around attempts to date the sequence, including isotopic age determinations on the overlying Kalokwanya Basalt, as well as biostratigraphic comparisons.

The systematic field work undertaken by the National Museums of Kenya in the early 1990s, under the direction of M. G. Leakey, led to important new fossil discoveries, a reinvestigation of the sedimentary sequence, and establishment of detailed chronostratigraphic control (Leakey et al., 1995, 1998). A detailed analysis of the numerous paleosols in the Kanapoi sequence was reported by Wynn (2000).

EXPOSURE AND STRUCTURE

The entire sedimentary sequence at Kanapoi dips very gently (~1°) to the west. Local depositional dips, however, can be quite high. These are commonly 12–15° at some distance above the basement, and may reach 45° where sediments are draped directly over hills in the volcanic basement. Several small faults (0.5–1.0 m offset) occur in the study area, and in the southeast, a more significant normal fault (bearing 310°, down to NE) offsets the section by several tens of meters. For the most part, however, the sequence is much more strongly affected by deposition over pre-existing topography than by subsequent tectonics.

THE KANAPOI FORMATION

The Pliocene sedimentary rocks exposed in the Kanapoi region (Fig. 1) are here defined as the Kanapoi Formation. The type section of the formation, section CSF 95-8 (Fig. 2), is located in the southeastern part of the exposures and displays most of the major characteristics of the formation. Where exposed, the base of the formation rests unconformably on Mio–Pliocene basalts. The Pliocene Kalokwanya Basalt unconformably caps the formation. In the type section, the Kanapoi Formation is 37.3 m thick. Some local sections are known to reach nearly 60 m in thickness, and the formation can be seen to pinch out entirely between the basalts to the east and north.

The new formation designation is justified on both lithostratigraphic and historical grounds. The formation is mappable and lithologically distinctive. Unifying characteristics include the dominance of paleotopographic influence in sedimentary accumulation pattern and an early basaltic clast dominance later replaced by silicic volcanics. The single tephrostratigraphic marker within the formation that has been geochemically characterized is the Kanapoi Tuff (Leakey et al., 1998). The formation is related to synchronic deposits of the Turkana basin farther north, but historical usage, complex relationships, and lack of correlative marker tephra (boundary stratotypes) preclude assignment to any previously defined stratigraphic units. The lower portion of the formation likely correlates with the upper Apak Member of the Nachukui Formation described from Lothagam (Feibel, 2003). The lacustrine interval in the middle of the Kanapoi Formation is correlative with the lower Lonyumun Member of the Nachukui and Koobi Fora Formations (Brown and Feibel, 1986; Harris et al., 1988). The upper sedimentary interval in the Kanapoi Formation corresponds broadly to lower members of the Omo Group formations to the north (Moiti and Lokochot Members of the Koobi Fora Formation or Kataboi Member of the Nachukui Formation).

Three tephra units within the Kanapoi Formation have been isotopically dated. Two devitrified pumiceous tephra low in the sequence yielded ages of 4.17 ± 0.03 Ma (lower pumiceous tuff) and 4.12 ± 0.02 Ma (upper pumiceous tuff) (Leakey et al., 1995), while the vitric Kanapoi Tuff was found to contain rare pumices, which were dated to 4.07 ± 0.02 Ma (Leakey et al., 1998). In addition, the overlying Kalokwanya Basalt has been dated to 3.4 Ma, providing an upper limit on the age of the formation. The onset of accumulation is estimated to have begun around 4.3 Ma. Most of the subconglomeratic sequence likely accumulated prior to 3.9 Ma, but the sedimentary environments responsible for accumulation of the uppermost Kanapoi strata were likely active up until extrusion of the Kalokwanya Basalt.

The Kanapoi sedimentary sequence was deposited on a dissected volcanic landscape with at least 40 m of local relief. This basal topography had a strong influence on the lateral variability of the sequence and disrupted the sedimentation pattern through nearly the entire stratigraphic thickness. The lowermost stratigraphic units are localized within paleotopographic lows, while the superposed strata become more and more laterally continuous upwards. The onlapping sequence of sediments is complex, as the strata were deposited more-or-less horizontally, against this topographic surface. The overall stratigraphic sequence of the Kanapoi Formation reflects three intervals, an initial fluvial regime, a subsequent lacustrine phase, and a final return to fluvial conditions.

Local basement for the Kanapoi Formation consists of Mio–Pliocene basalts. They are typically spheroidally weathered, and present a landscape of conical hills, many of which protrude through the eroding sedimentary sequence today (Fig. 1). There is considerable variation in the nature of the contact between the local basement and the Kanapoi Formation, primarily as a function of paleotopographic position. The most common association, seen in paleotopographic lows as well as at other positions, is a scoured relationship, which superposes basalt cobble- to pebble-conglomerates, or less frequently sandstones, on basalt basement (Fig. 2: sections CSF 95-8, 95-10). Slightly higher paleotopographic positions sometimes preserve a gravel

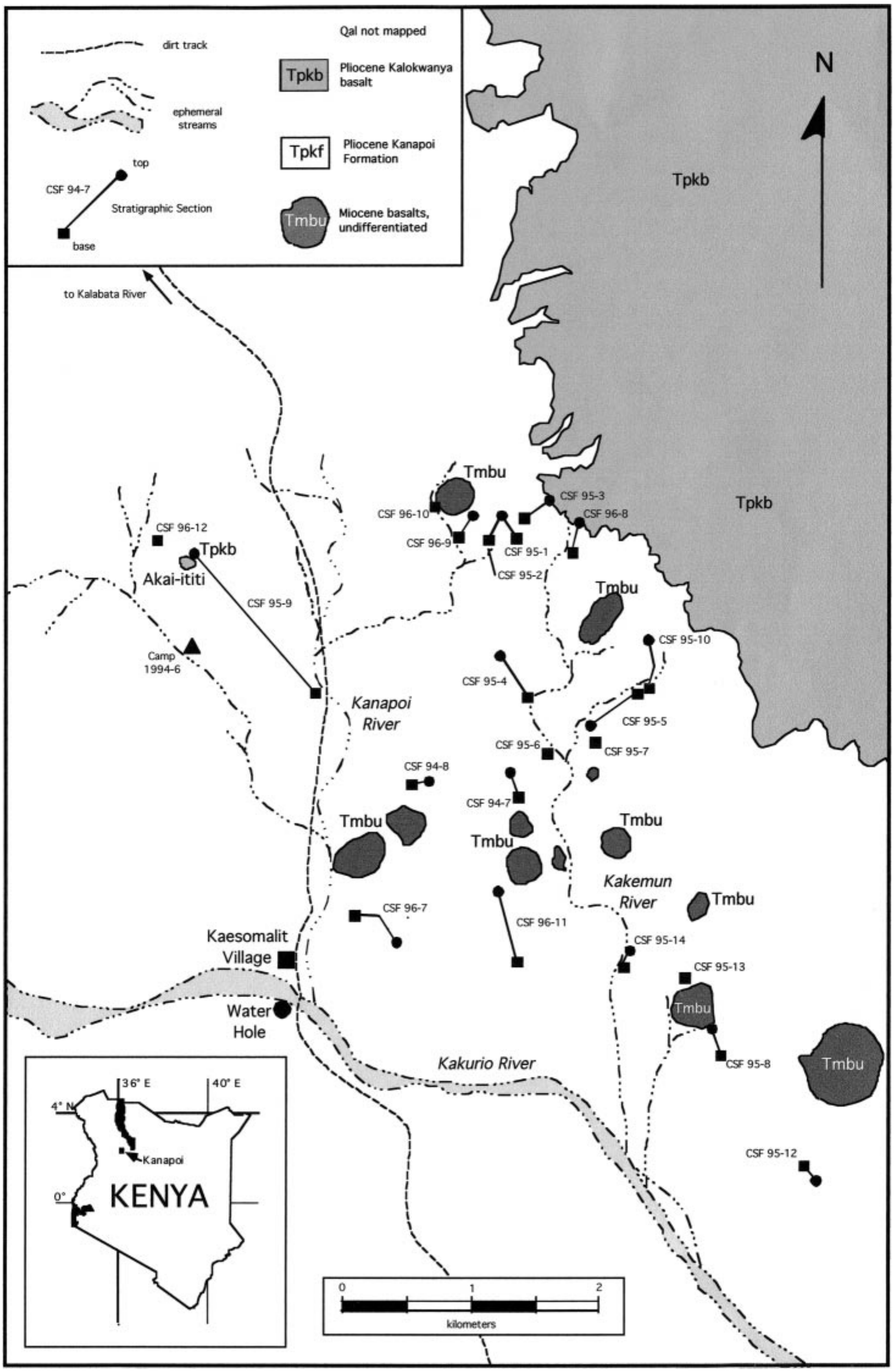

Figure 1 Geological map of the Kanapoi area showing prominent geographic landmarks and locations of the stratigraphic sections

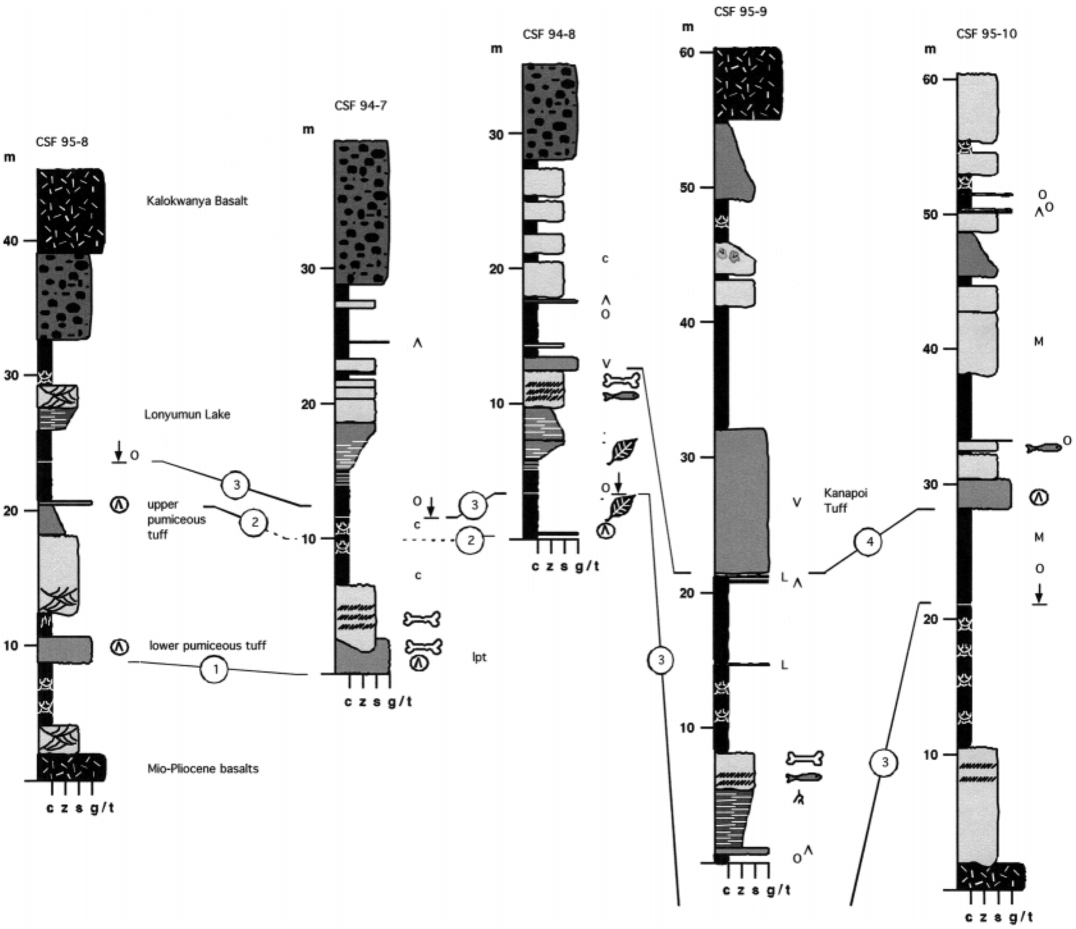

Figure 2 Type section (CSF 95-8) and reference sections of the Kanapoi Formation. Numbered correlations shown are 1, lower pumiceous tuff; 2, upper pumiceous tuff; 3, basal flooding surface of the Lonyumun Lake sequence; and 4, Kanapoi Tuff. See Figure 1 for location of sections. For a key to symbols, see Figure 3

regolith developed on the basalt, along with a blocky structured paleosol developed on silts or clays (Fig. 4; sections CSF 96-10, 95-13). At even higher paleotopographic positions, corresponding to the landscape exposed at the time of inundation by the Lonyumun Lake, molluskan packstones representing bioherms up to 1 m in thickness are developed on what were then islands of the basalt basement. The highest of the paleotopographic hills preserves a pebbly clay paleosol that has been contact baked upon extrusion of the capping Kalokwanya Basalt (east of CSF 96-8).

The initial sedimentary interval of the Kanapoi Formation, informally termed the lower fluvial sequence, can be constrained between the Mio–Pliocene basalts below and the lacustrine sequence above. The base of the lacustrine sequence is a sharp boundary in virtually all sections and is easily recognizable by an abundance of ostracods, carbonized plant fragments, and/or mollusks. The lower fluvial sequence is characterized by conglomerates, sandstones, and claystones with well-developed vertic (paleosol) structure. The conglomerates are generally massive, basalt cobble to pebble units. Sandstones are medium- to fine-grained, quartzofeldspathic or litharenitic, and commonly display well-developed planar crossbedding in 10–20 cm bedsets. Large-scale trough crossbedding is locally seen in coarser sandstones, while the finer grained sands and upper portions of sand bodies are typically massive due to bioturbation. Mudstones are generally quite thick in the lower fluvial sequence (up to 10 m; sections CSF 95-10 in Fig. 2 and 95-5 in Fig. 5), with well-developed paleosols. Wynn (2000) has provided a detailed analysis of paleosols throughout the formation. The most common paleosol is the Aberegaiya pedotype, a thick, often cumulative vertisol with well-developed wedge-shaped peds and slickensided dish fractures. This lower sedimentary sequence records a depositional regime controlled by fluvial systems, and

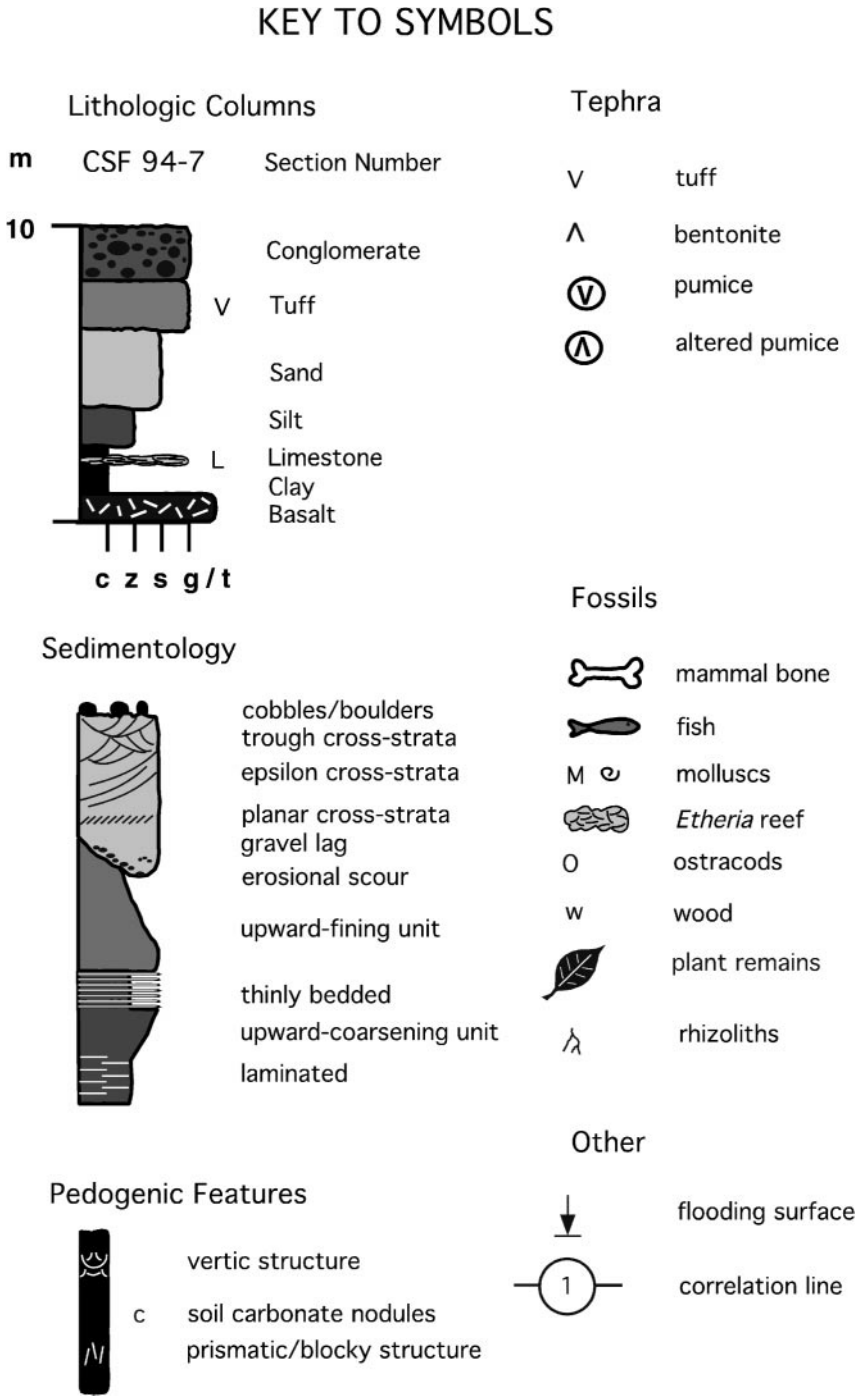

Figure 3 Key to symbols for the graphic sections presented in this report

there are indications of both braided and meandering streams based on internal sequences and primary structures.

Several tephra units are intercalated within the lower fluvial sequence. The two most prominent of these display characteristics of airfall tephra that mantled the Kanapoi paleolandscape. The lower pumiceous tephra layer is a thick (up to 3.6 m), poorly sorted unit, with altered angular pumice clasts to 1 cm in diameter scattered throughout.

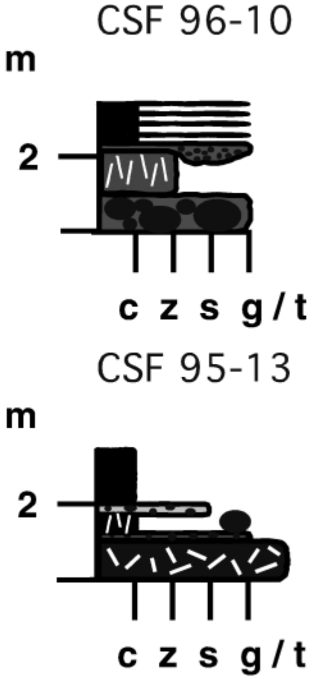

Figure 4 Reference sections from the basal contact of the Kanapoi Formation. See Figure 1 for location of sections. For a key to symbols, see Figure 3.

The upper pumiceous tephra layer is a thinner unit (ca. 15 cm), and displays laminated basal and upper subunits with an unsorted pumiceous middle. The vitric component of these tephra has been completely altered to clay and zeolite minerals. Both, however, had a significant pumiceous component. The pumices have been devitrified and slightly flattened, but appear as clay pebbles dispersed throughout the units. Devitrification of the pumices has left a residual population of volcanogenic feldspar crystals, which have been used to control for the age of the strata and associated fossils.

Overlying the lower fluvial sequence and locally banked against the higher elements of the eroded volcanic basement is a lacustrine interval. Lithostratigraphic, chronostratigraphic, and biofacies indicators all support correlation of this lacustrine interval with the Lonyumun Lake phase well known from the Omo Group deposits of the northern Turkana Basin (Brown and Feibel, 1991; Feibel et al., 1991) as well as from Lothagam (Feibel, 2003) and elsewhere in the lower Kerio Valley (Feibel, unpublished). Where the volcanic basement produced local islands in this lake, they are mantled by a molluskan packstone, dominated by the gastropod *Bellamya* Jousseaume, 1886. Elsewhere, the lacustrine strata begin with a mollusk- and ostracod-rich claystone, typically succeeded by a well-laminated claystone and siltstone sequence, and continue with an upward coarsening sequence, which is capped by distributary channel sands. The upper portion of the deltaic complex has isolated sand bodies, representing distributary channels. This deltaic complex contains the only vitric tuff preserved at Kanapoi. This unit, termed the Kanapoi Tuff (Leakey et al., 1998), is a pale brown, fine-grained tuff with well-preserved climbing-ripple cross-lamination. Upper portions of the tuff commonly show soft-sediment deformation, and in a few localities, the tuff preserves pumice. The composition of this tephra indicates an iron-rich rhyolite (Table 1). Although this tephra does not correlate with any of the well-known tephra of the Turkana Basin Omo Group sequence, Namwamba (1993) has suggested that it correlates with his Suteijun Tuff of the Chemeron Formation in the Baringo Basin to the south.

Above the Kanapoi Tuff, lacustrine conditions persisted locally for a short period. In an important locality west of Akai-ititi, a distributary channel sequence is cut into the Kanapoi Tuff (Fig. 6). Here the eroded channel base is draped with a molluskan packstone that includes a well-developed reef of the Nile oyster *Etheria* Lamarck, 1807. The remainder of the channel is filled with a quartzofeldspathic sand. The record of *Etheria* in a channel setting documents the perennial nature of the river at this time. The transition from the lacustrine interval to the upper fluvial interval is not sharp, as in the base of the lacustrine sequence, but rather proceeds through an interval of interbedded shallow lacustrine muds and those with a clear pedogenic overprint indicating exposure. There are also several moderate to well-developed paleosols within the lacustrine sequence, indicative of instability in lake-level as well as local emergence due to delta progradation. Wynn (2000) reports several new pedotypes from this stratigraphic interval due to these particular conditions.

In most sections, the overlying sedimentary sequence again becomes dominated by a fluvial system, and several coarse gravels with significant erosional bases cap the sedimentary deposits. This interval is referred to here as the upper fluvial sequence. Like the lower fluvial sequence, this interval exhibits a high degree of lateral variation (Fig. 7). The influence of the basement topography is considerably less, however, and thus the sequence presents more characteristic upward-fining units indicative of a meandering fluvial system. It is noteworthy that, in all but one section, once fully fluvial conditions are re-established, there is no further indication of lacustrine conditions or even of floodplain ponding. The single exception is seen in section CSF 95-10 (Fig. 2). Here a thin interval of ostracod-packed claystones and fissile green claystones clearly indicates deposition in a lake or pond. This interval rests on a thin bentonite. It is possible that this sequence represents the Lokochot Lake, a lacustrine phase, which occurred ca. 3.5 Ma in the Turkana Basin. The Lokochot Lake is well documented from Omo Group deposits in the northern Turkana Basin

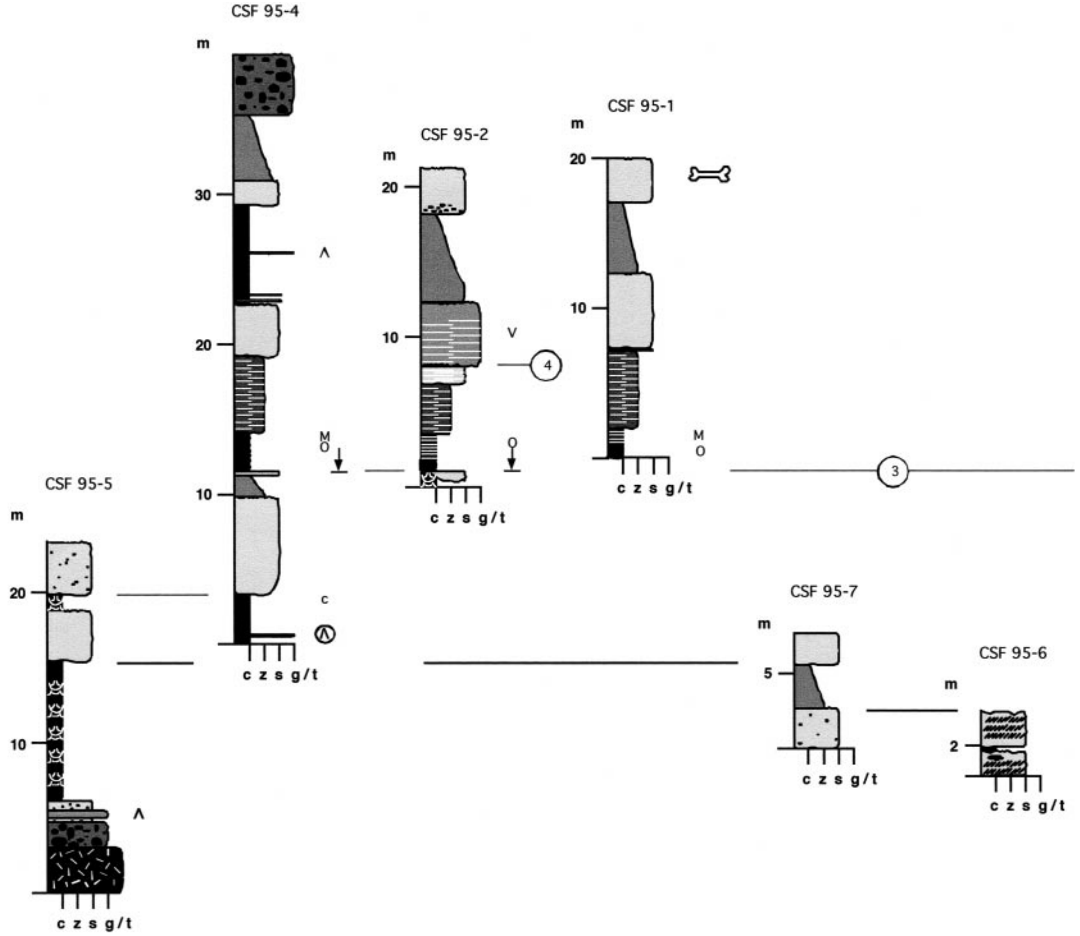

Figure 5 Reference sections from the lower and middle portions of the Kanapoi Formation. Numbered correlations shown are 3, basal flooding surface of the Lonyumun Lake sequence; and 4, Kanapoi Tuff. Unnumbered correlations are lithologic contacts walked out between sections. See Figure 1 for location of sections. For a key to symbols, see Figure 3

(Brown and Feibel, 1991; Feibel et al., 1991), and has been recognized elsewhere in the lower Kerio Valley (Feibel, unpublished).

The uppermost strata of the Kanapoi Formation are a sequence of massive cobble- to pebble-conglomerates, which incise deeply into the underlying fluvial strata. These conglomerates are dominated by silicic volcanics, with a matrix of litharenite sand. The conglomerates may occur as multiple units and may reach up to 21 m in thickness. They often have thin sand interbeds. Mudstones are rare in this upper part of the section, and by the top of the formation, the depositional setting appears to have developed into a gravel braidplain. These gravels are overlain by the Kalokwanya Basalt (Powers, 1980). The basalt has been dated to 3.4 Ma by McDougall (Leakey et al., 1995). In some localities, the basalt fills deep channels cut into the conglomerates.

The vertical and lateral variations in lithofacies

Table 1 Electron microprobe analysis of glass from the Kanapoi Tuff (Leakey et al. 1998).[a]

Sample	SiO_2	Al_2O_3	Fe_2O_3	CaO	K_2O	Na_2O	MgO	MnO	TiO_2	Cl	F	Zr	Total	N
KP01-15-01	70.36	7.86	8.32	0.37	3.93	1.73	0.01	0.25	0.25	0.42	0.03	NA	93.53	6
K92-4846	69.50	7.55	8.31	0.28	0.26	0.16	0.01	0.25	0.23	0.52	0.01	0.29	96.49	13
K92-4847	69.76	7.66	8.42	0.29	0.37	0.24	0.01	0.25	0.24	0.48	0.01	0.28	96.58	18

[a] Abundances are shown as weight per cent. N, number of shards analyzed; NA, not analyzed

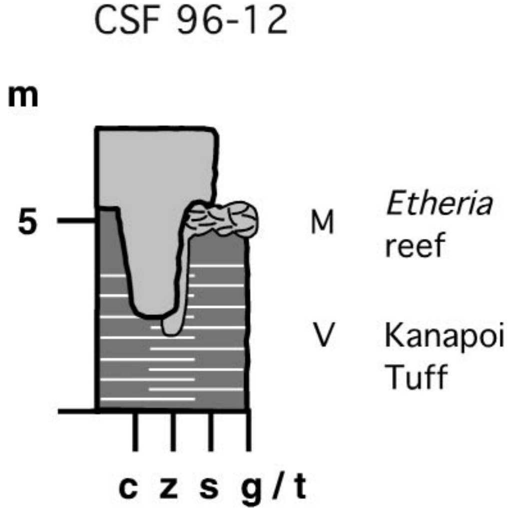

Figure 6 Reference section from the middle portion of the Kanapoi Formation. The Kanapoi Tuff here is deeply channeled, and the channel-fill includes both an *Etheria* bioherm and a later channel sand. See Figure 1 for location of sections. For a key to symbols, see Figure 3

seen at Kanapoi are summarized in Figure 8. This somewhat schematic diagram emphasizes the geometry of the major facies types and their relationships to the underlying basement paleotopography.

FOSSIL CONTEXT AND PALEOENVIRONMENTS

The Kanapoi stratigraphic sequence is summarized in the composite section of Figure 9. This composite forms the basis for a discussion of the context of fossil vertebrate faunas recovered from Kanapoi, as well as for the environmental history recorded in the deposits.

There are two major stratigraphic levels producing the bulk of the vertebrate fossil material at Kanapoi. The lower level is the channel sandstone and overbank mudstone complex associated with the lower and upper pumiceous tephra. Most of the fossils in this interval, including much of the *Australopithecus anamensis* Leakey et al., 1995, hypodigm, come from vertic paleosols developed on the floodplain through this period. The upper fossiliferous zone is the distributary channel complex associated with the Kanapoi Tuff. This richly fossiliferous zone is dominated by aquatic forms (fish and reptiles) but also includes a wide range of terrestrial mammals. Fossils are also found in the upper fluvial sequence, where they are associated with both channel and floodplain settings.

The environmental setting recorded by the Kan-

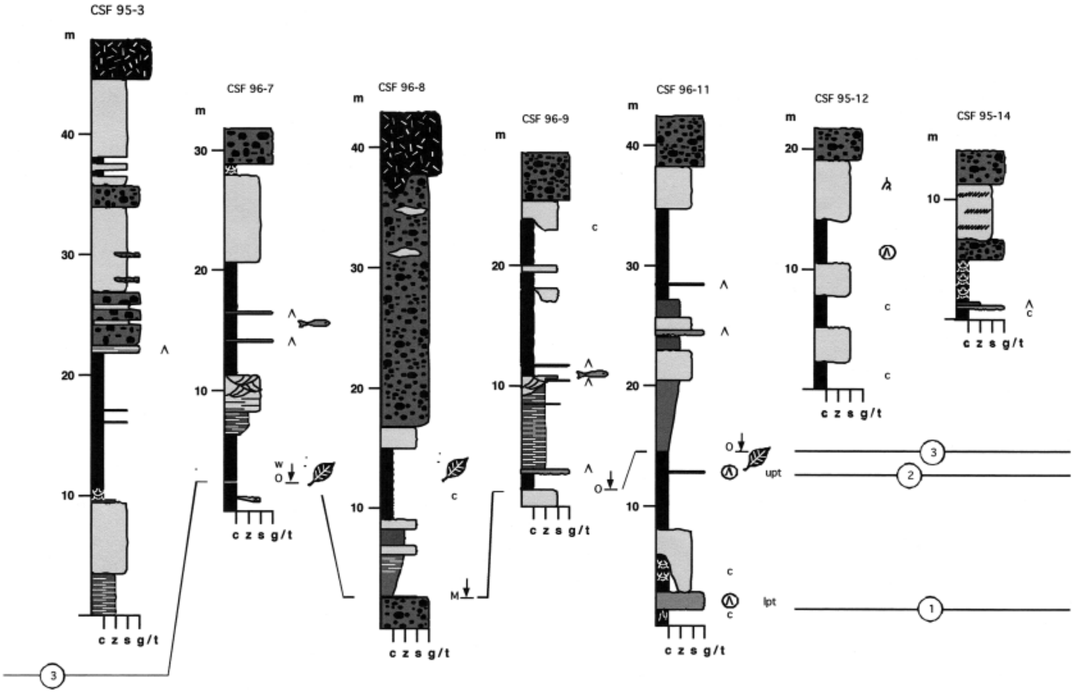

Figure 7 Reference sections from the upper part of the Kanapoi Formation. Numbered correlations shown are 1, lower pumiceous tuff; 2, upper pumiceous tuff; and 3, basal flooding surface of the Lonyumun Lake sequence. See Figure 1 for location of sections. For a key to symbols, see Figure 3

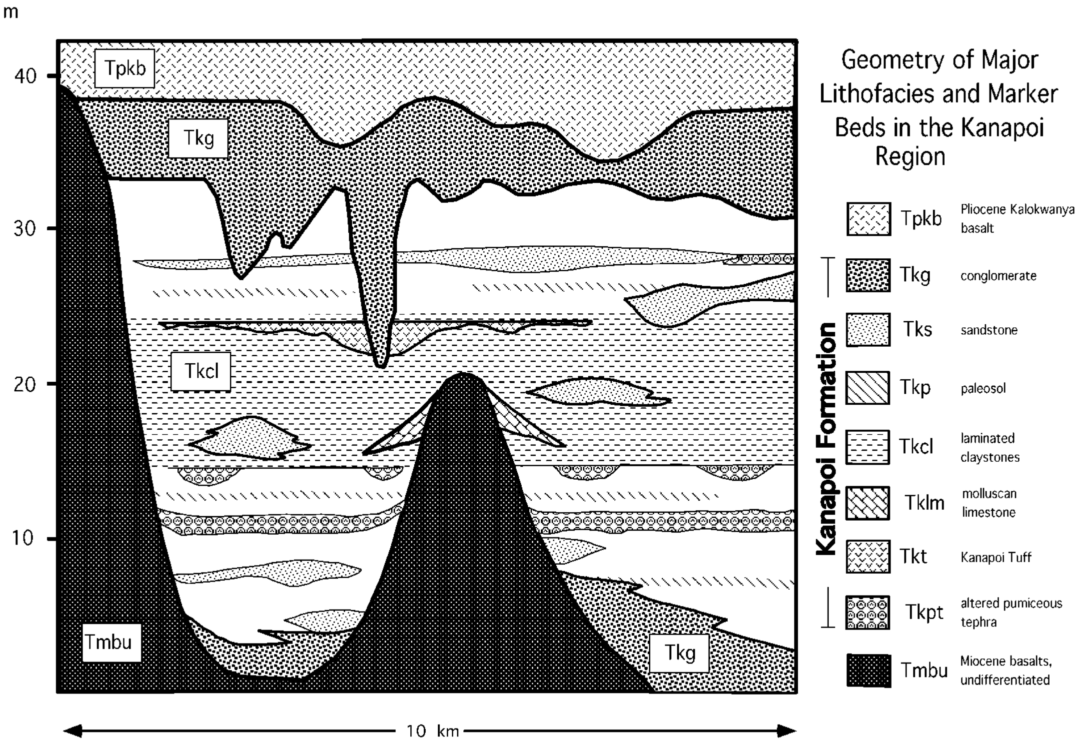

Figure 8 Schematic drawing of the geometry of major lithofacies and marker beds in the Kanapoi Formation. Note the vertical exaggeration in the diagram. Only major components are depicted, minor facies are shown in white

apoi sedimentary sequence reflects a progression of fluvial and lacustrine systems that overwhelmed a volcanic landscape. The fluvial system that dominated local environments throughout the Kanapoi record was the ancestral Kerio River. This is supported by evidence from the tectonic heritage of the region, provenance of sedimentary clasts, and the southerly link provided by correlation of the Kanapoi Tuff into the Baringo Basin. The ancestral Kerio River was certainly seasonal through this time period. Perennial flow is only demonstrated for the middle of the represented time interval, through the presence of *Etheria* reefs in a channel setting above the Kanapoi Tuff. At other times, there are indicators of strong seasonality in flow, particularly in conglomerates low and high in the section as well as in the prevalence of planar cross-stratification in many of the sands. This may reflect strong seasonality in a perennial stream or ephemeral flow conditions. The well-developed upward-fining cycles, particularly in the upper fluvial interval, however, are suggestive of continued perennial flow there.

The hills/islands of the volcanic basement provided a considerable degree of local heterogeneity. For the fluvial systems, this would have been manifest not only in the local topographic relief but also in different soil conditions, drainage, and vegetation patterns. This is an element of habitat patchiness which is not typically seen in the Plio–Pleistocene paleoenvironments investigated from elsewhere in the Turkana Basin (e.g., Feibel et al., 1991). The fluvial systems that encountered this complex landscape were spatially controlled by paleotopographic lows that restricted both the flow patterns for fluvial channels as well as the extent and connectedness of the early floodplains. Although the degree of influence this basement topography exerted decreased through time, it was present throughout the formation.

A strong seasonality in precipitation is documented by the prevalence of vertisols in the overbank deposits. In this sense, the Kanapoi floodplains are closely comparable with those of the early Omo Group sequence (e.g., Moiti, Lokochot, Tulu Bor Members) in the Turkana Basin to the north. There does not appear to be a progressive shift in the character of paleosols through time at Kanapoi. Rather, the variability seen in soil types reflects aspects of the soil catena across the Kanapoi paleolandscape. This relates primarily to topographic effects (including drainage and leaching), soil development on different parent materials, and variations in the maturity of soils induced by reorganizations of the landscape. Examples of the latter are the influence tephra fallouts produced in the lower and upper pumiceous tephra. The pervasive

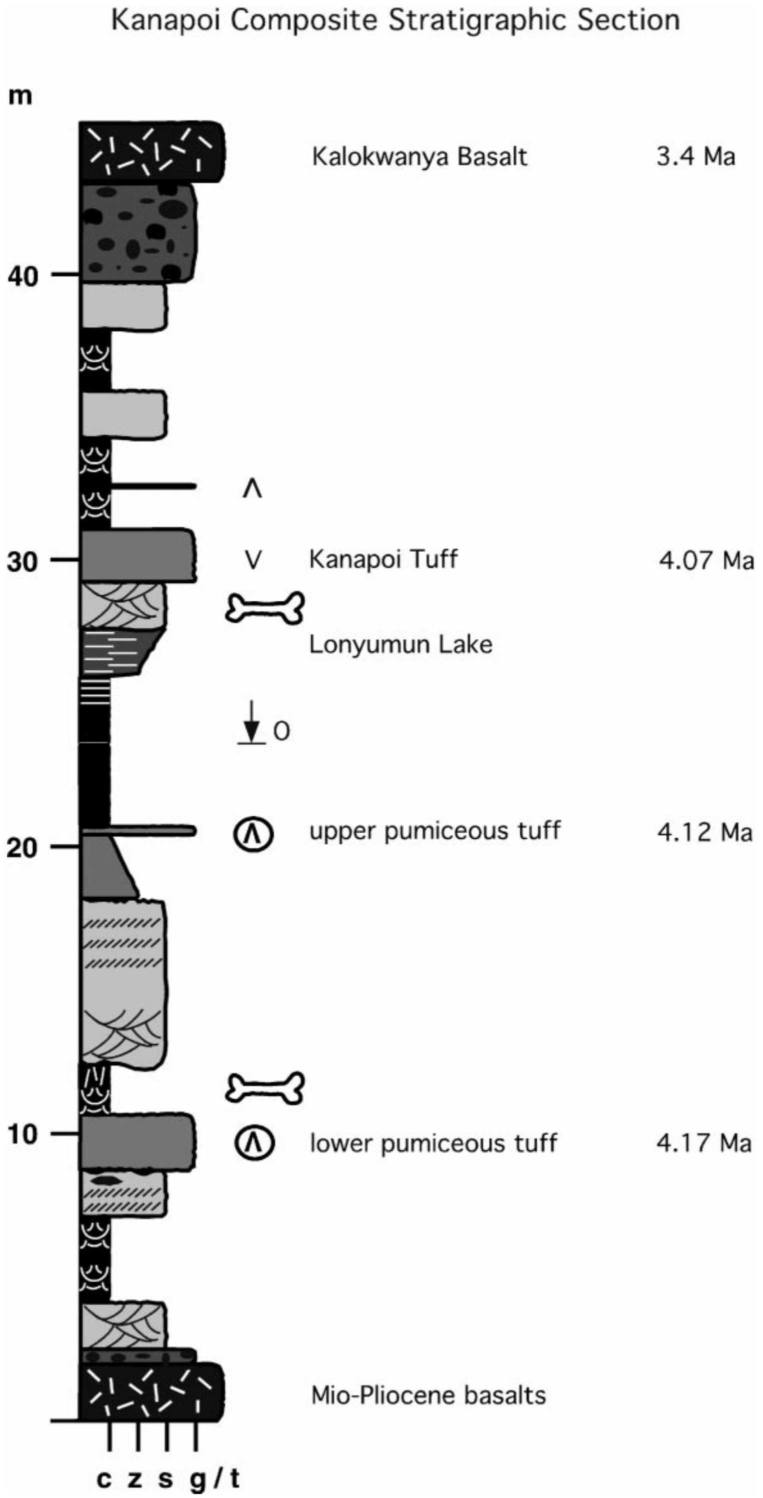

Figure 9 Composite stratigraphic column for the Kanapoi Formation. Note major fossiliferous levels in lower fluvial paleosols and in deltaic sands of the Lonyumun Lake stage. Age control based on work of I. McDougall (Leakey et al., 1995, 1998)

thick profile of the lower pumiceous tephra indicates it blanketed the landscape and would have forced a 'restart' of a successional regime in soil, vegetation, and ecological communities based on this volcanic parent matter. The thinner upper pumiceous tephra is only patchily preserved, which implies that it was locally incorporated into the active soil substrate rather than overwhelming it.

The Lonyumun Lake transgression produced the most dramatic reorganization of the Kanapoi landscape. The sharp basal contact of the lacustrine claystone in this interval demonstrates a rapid drowning of the landscape. The precise chronostratigraphic control on the Kanapoi sequence provides the best age control on this event, which can be placed at 4.10 ± 0.02 Ma. The Lonyumun transgression affected a major portion of the Turkana Basin (ca. 28,000 km^2), most likely due to tectonic or volcanic damming of the basin outlet. The transgression was everywhere rapid, and Kanapoi is situated along the drowned paleovalley into which the ancestral Kerio River flowed.

The rapid local infilling of the Lonyumun Lake at Kanapoi is to be expected from the minimal accommodation space available in this drowned paleovalley and the rapid sedimentation induced by proximity of the ancestral Kerio River Delta. The thick accumulation of the Kanapoi Tuff (nearly 11 m) in the central part of the Kanapoi area resulted from the filling of the interdistributary bays of this delta (Powers 1980) following an explosive eruption in the rift valley to the south. As the lake retreated northwards, a progression of minor inundations and exposure is reflected in the interbedded fluvial and lacustrine strata that mark the transition from the lacustrine phase to the upper fluvial sequence.

The characteristics of the fluvial strata that succeeded the Lonyumun Lake sequence reflect the considerable infilling that the lake phase produced and the broader floodplains available for a meandering river system. In other aspects, however, this river was very similar to the system that existed prior to the Lonyumun transgression. This lower portion of the upper fluvial sequence stands in stark contrast, however, to the upper strata of the interval, where sands and gravels dominate to the near exclusion of mudstones. This upper portion of the formation reflects two fundamental changes in the system, increased supply of coarse clastics and a gradual drop-off in overall accumulation rates. The clastics are dominated by siliceous volcanic cobbles and pebbles, in contrast to the basaltic suite of conglomerates at the base of the formation. This likely reflects renewed tectonic activity in the source area to the south. The slowdown in accumulation is implied rather than measured, as there are no time markers between the Kanapoi Tuff and the Kalokwanya Basalt. The dramatic change in sedimentary facies, however, suggests that much of the time between these two chronostratigraphic markers lies within these upper gravels. This upper portion of the sequence would likely have presented the most dramatic deviation in environmental characteristics. The substrate of the braidplain would have been well drained, and the coarse siliceous volcanics would provide a poor medium for growth of vegetation. The starkness of this landscape would be succeeded, however, by the truly inhospitable volcanic landscape produced by eruption of the Kalokwanya Basalt.

CONCLUSIONS

The Pliocene sedimentary sequence of the Kanapoi region, termed here the Kanapoi Formation, was deposited by the ancestral Kerio River in three phases. Initial deposition occurred upon a fluvial floodplain that was broken by numerous hills of the local Mio–Pliocene basaltic basement. These hills strongly influenced patterns of deposition, as the fluvial system mantled the complex topography with channel gravels and sands, while vertic paleosols developed on the adjacent floodplains. Two pumiceous airfall tephra accumulated on this landscape (lower pumiceous tuff, 4.17 Ma; upper pumiceous tuff, 4.12 Ma), allowing precise chronostratigraphic control on this phase of deposition. The Lonyumun Lake transgression replaced the fluvial system with a lacustrine setting and the rapidly prograding Kerio River Delta. The vitric Kanapoi Tuff (4.07 Ma) was deposited primarily in interdistributary floodbasins at this stage. The progradation locally replaced the Lonyumun Lake with a second floodplain system, somewhat less constrained by basement topography. A shift in this system from a meandering sand/mud fluvial system to a gravel braidplain reflects tectonic activity in the source area to the south and a lowering of accumulation rates. Eruption of the Kalokwanya Basalt effectively ended significant sediment accumulation at Kanapoi.

The rich vertebrate fossil assemblages of Kanapoi are found in floodplain paleosols of the lower and upper fluvial intervals, as well as in the distributary sands of the Kerio River Delta during the Lonyumun Lake phase. The high degree of landscape heterogeneity and pronounced soil catenas of the Kanapoi setting provided some of the greatest habitat patchiness recorded from the Turkana Basin Plio–Pleistocene.

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FOSSIL FISH REMAINS FROM THE PLIOCENE KANAPOI SITE, KENYA

KATHLYN STEWART[1]

ABSTRACT. Over 2,800 fossil fish elements were collected in the 1990s from the Pliocene site of Kanapoi, located in the Turkana Basin, northern Kenya. The Kanapoi fish fauna is dominated by large piscivores and medium to large molluscivores, whereas herbivorous fish are rare. The genera *Labeo, Hydrocynus,* and *Sindacharax* are abundant in the deposits, as are large percoids and catfish. While the Kanapoi fauna has many similarities with both the near-contemporaneous fauna recovered from the Muruongori Member at nearby Lothagam and the site of Ekora, including the extinct genera *Sindacharax* and *Semlikiichthys,* it differs significantly in two features. The Kanapoi fauna is dominated by a *Sindacharax* species that is absent at Muruongori and it lacks two other *Sindacharax* and two *Tetraodon* species which are common in the Muruongori deposits and at Ekora. The Kanapoi fauna is similar to that from the Apak Member at Lothagam, in particular by the domination of *Sindacharax mutetii.*

INTRODUCTION

The presence of fossil fishes at Kanapoi had been reported by Behrensmeyer (1976) among others, but no systematic recovery was initiated until 1993. Over 2,800 fossil fish elements were recovered from Kanapoi deposits in the 1993 and 1995 field seasons (see map in Introduction, page 2). Most collecting was undertaken by the author and Sam N. Muteti, of the National Museums of Kenya, with some additional collecting by the National Museums of Kenya fossil team. As discussed by Feibel (2003b), the major phase of deposition of the Kanapoi deposits date from 4.17 Ma to about 4.07 Ma with three sedimentary intervals: a lower fluvial sequence, a lacustrine phase, and an upper fluvial sequence. The fish fossils were collected from six sites located in the lacustrine phase of the formation, and from one site probably deposited during the upper fluvial sequence and hence slightly younger than 4.07 Ma.

Fieldwork at Kanapoi followed three years of intensive collection of vertebrate and invertebrate fossils from the nearby site of Lothagam (Leakey et al., 1976; Leakey and Harris, 2003), with fossiliferous deposits ranging in age from late Miocene to Holocene, as well as from the western Turkana Basin Pliocene sites of Ekora, South Turkwel, North Napudet and Eshoa Kakurongori. Reference will be made in this report to the detailed description of over 7000 fish fossils collected at the nearby site of Lothagam (Stewart, 2003). Collection of fish fossils at Lothagam was extensive, in order to obtain information on systematics, environment and biogeography, previously poorly known from this period. Most fish elements collected from Lothagam derived from the Lower and Upper Nawata Members of the Nawata Formation, and the Apak Member of the Nachukui Formation, ranging in age from 7.44 Ma to about 4.2 Ma (McDougall and Feibel, 1999). Fish bones were also collected from the Muruongori Member, and the Kaiyumung Member of the Nachukui Formation, which date to about 4.0 Ma, and approximately 4.0 to 2.0 Ma respectively (C. Feibel, F. Brown, personal communication). More detailed information about the stratigraphy and geochronology at Lothagam is provided by Feibel (2003a) and McDougall and Feibel (1999).

Fish collecting at Kanapoi was less extensive than at Lothagam, as only elements with potential taxonomic and systematic information were collected. The Kanapoi fish elements derive from sediments which date close to 4.07 Ma, and, like the Muruongori Member sediments at Lothagam, were probably deposited during the Lonyumun Lake transgression (Feibel, 2003b). Reference will also be made to the fish collected from the Ekora site, located about 50 km southeast of Lothagam and about 25 km north of Kanapoi, near the modern Kerio River. The Ekora fauna is of Pliocene age and probably also derives from Lonyumun Lake deposits (Feibel, personal communication).

In the descriptions and discussions below, ecological and zoogeographical information on modern fish was referenced from the *Checklist of the Freshwater Fishes of Africa* volumes (Daget et al., 1984, 1986) and from Hopson and Hopson (1982).

The Kanapoi fishes have not yet been accessioned into the collections of the National Museums of Kenya. In the systematic description, the specimens are listed by the field number for their site of origin.

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Natural History Museum of Los Angeles County, 2003

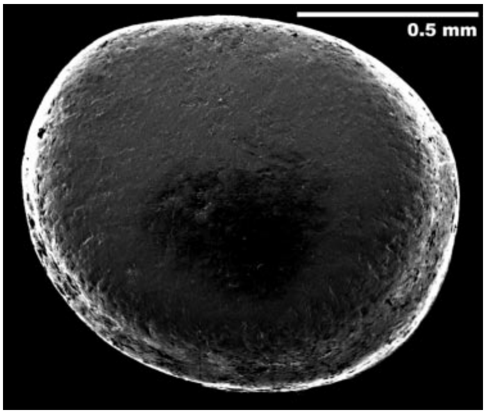

Figure 1 *Hyperopisus* sp., SEM of isolated tooth, ventral view, from Kanapoi

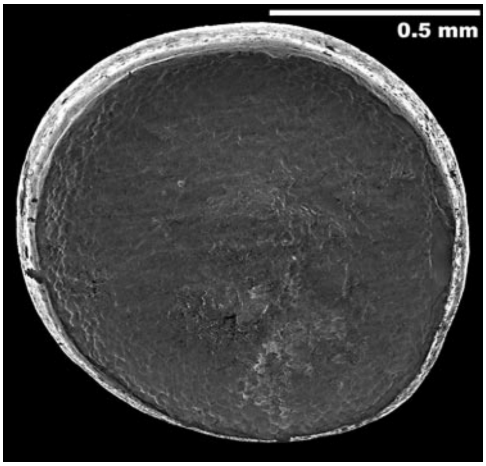

Figure 2 *Hyperopisus* sp., SEM of isolated tooth and base, dorsal view, from Kanapoi

SYSTEMATIC DESCRIPTION

Order Polypteriformes

Family Polypteridae

Polypterus Geoffroy Saint-Hilaire, 1802

Polypterus sp.

KANAPOI MATERIAL. 3156, scale.

Polypterus material is extremely rare in Kanapoi deposits, with only one element identified. As *Polypterus* scales, spines, and cranial fragments are robust and preserve well, this poor record suggests a minimal Pliocene presence at Kanapoi.

The family Polypteridae is today represented by two genera: *Polypterus* and *Calamoichthys* Smith, 1866 (rather than *Erpetoichthys* Smith, 1865; see discussion in Stewart, 2001), both restricted to Africa. Most fossil elements comprise scales, vertebrae, and spines, and have been referred to the larger and today much more widely distributed genus *Polypterus* or only to the family Polypteridae.

Polypterus is a long, slender fish with a distinctive, long dorsal fin that is divided by spines into portions resembling sails; they have a lung-like organ to breathe air. Polypteridae have several primitive features with similarities to Paleozoic paleoniscoids (Carroll, 1988). Their earliest fossil record from Africa is from Upper Cretaceous deposits in Egypt, Morocco, Niger, and Sudan (Strömer, 1916; Dutheil, 1999). Their Cenozoic record includes fossils from Eocene deposits in Libya (Lavocat, 1955); Miocene deposits in Rusinga, Loperot, and Lothagam, Kenya (Greenwood, 1951; Van Couvering, 1977; Stewart, 2003), and Bled ed Douarah, Tunisia (Greenwood, 1973); Pliocene deposits at Wadi Natrun, Egypt (Greenwood, 1972); Pliocene deposits at Lothagam, Kenya (Stewart, 2003); and Plio–Pleistocene deposits at Koobi Fora (Schwartz, 1983). *Polypterus* has never been recovered from the Western Rift sites. Two extant species are known from Lake Turkana—*P. senegalus* Cuvier, 1829, and *P. bichir* Geoffroy Saint Hilaire, 1802. *Polypterus* is widespread from Senegal to the Nile Basin up to Lake Albert, as well as the Congo Basin and Lake Tanganyika.

Order Mormyriformes

Family Mormyridae

Hyperopisus Gill, 1862

Hyperopisus sp.

Figures 1, 2

KANAPOI MATERIAL. 3156, 1 tooth; 3845, 96 teeth; 3847, 7 teeth; 3848, 3 teeth; 3849, 2 teeth.

Hyperopisus teeth appear as truncated cylinders with smooth, relatively flat tops and bases (Figs. 1, 2), and attach to the parasphenoid and basihyal bones. The average diameter of the Kanapoi teeth (1–4 mm) is within the range of large extant *Hyperopisus* individuals (up to 90 cm total length).

Hyperopisus teeth are relatively common throughout the Kanapoi deposits. While absent from the Nawata Formation deposits at Lothagam, the teeth are common in the Nachukui Formation deposits and at the Pliocene South Turkwell site (personal observation). Modern *Hyperopisus* (and other mormyroids) generate weak electromagnetic fields in order to sense their environment. They are therefore absent from modern Lake Turkana and other bodies of water with high salinity values, which apparently impede this sensory ability (Beadle, 1981).

Fossil *Hyperopisus* teeth (see summary in Stewart, 2001) are known from Pliocene deposits of Wadi Natrun, Egypt (Greenwood, 1972), from Plio–Pleistocene deposits in the Lakes Albert and Edward Basins (Greenwood and Howes, 1975;

Stewart, 1990), Mio–Pleistocene Lakes Albert and Edward Basins deposits (Van Neer, 1994), from Pliocene deposits at Lothagam (Stewart, 2003) and from Plio–Pleistocene deposits at Koobi Fora (Schwartz, 1983). Modern *H. bebe* Lacépède, 1803, is known from the Omo River Delta of Lake Turkana, and from the Senegal, Volta, Niger, Chad, and Nile Basins.

Large teeth referred to ?*Hyperopisus* have been reported in Pliocene Lake Edward Basin deposits and Pliocene Wadi Natrun deposits (Greenwood, 1972; Stewart, 1990, 2001). These teeth, although identical to those of modern *Hyperopisus,* far exceed the size range of modern teeth, and as no identified bone has been recovered with the teeth, their affiliation is problematic. These were not recovered in the Turkana Basin deposits, and to date have a restricted Nile River and Western Rift presence.

Family Gymnarchidae

Gymnarchus Cuvier, 1829

Gymnarchus sp.

KANAPOI MATERIAL. 3156, 18 teeth; 3845, 3 teeth; 3847, 3 teeth; 3848, 3 teeth; 3849, 7 teeth.

Gymnarchus teeth line the premaxilla and dentary. They are common throughout the Kanapoi deposits. The Kanapoi teeth average 3–4 mm in width, which is within the size range of large modern individuals (60–100 cm total length).

Gymnarchus is piscivorous, although mollusks and insects are also eaten. As in *Hyperopisus,* these fish use an electromagnetic field to sense the environment and are therefore intolerant of highly saline waters. *Gymnarchus* teeth are common throughout the Kanapoi deposits, as they are throughout the Lothagam deposits. Fossil elements are reported from Miocene–Pleistocene deposits in Lakes Albert and Edward Basins (Van Neer, 1994), Pliocene deposits in the Lakes Albert and Edward Basins (Stewart, 1990; Van Neer, 1992), late Miocene and Pliocene deposits at Lothagam, Kenya (Stewart, 2003), and Plio–Pleistocene deposits at Koobi Fora (Schwartz, 1983). Modern *G. niloticus* Cuvier, 1829, is known from the Omo River Delta in Lake Turkana, and in the Gambia, Senegal, Niger, Volta, Chad, and Nile Basins.

Order Cypriniformes

Family Cyprinidae

Labeo Cuvier, 1817

Labeo sp.

(Figures 3, 4)

Figure 3 *Labeo* sp., SEM of pharyngeal tooth, side view, from Kanapoi

KANAPOI MATERIAL. 3156, 12 teeth; 3845, 24 teeth; 3846, 4 teeth; 3847, 37 teeth; 3848, 6 teeth; 3849, 26 teeth teeth, 1 trunk vertebra.

Labeo is essentially represented by its pharyngeal teeth, which were not identifiable to species (Figs. 3, 4). One vertebra was also recovered, and while similar to *Barbus* Cuvier and Cloquet, 1816, vertebrae, *Labeo* vertebrae can be distinguished by trabecular morphology. These elements represent individuals up to 90 cm in total length, which is within the modern size range of the Turkana species.

Labeo teeth are surprisingly common throughout the Kanapoi deposits. Its teeth are rare in the Nawata Formation sites at Lothagam, but more com-

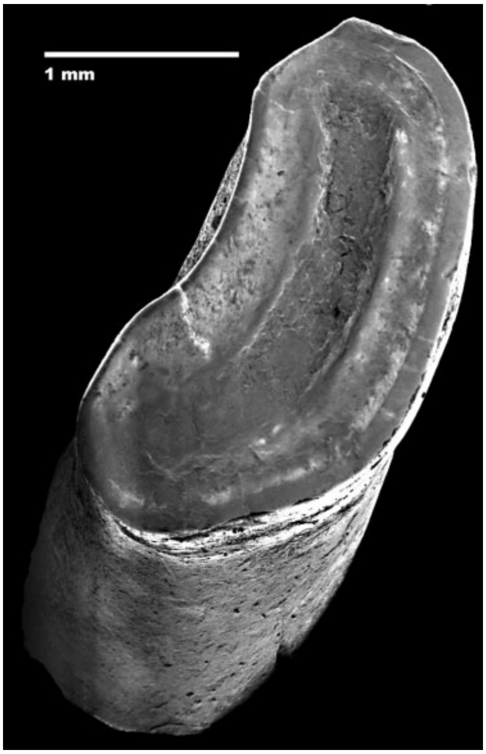

Figure 4 *Labeo* sp., SEM of pharyngeal tooth, ventral view, from Kanapoi

mon in the Nachukui Formation sites. *Labeo* is an inshore bottom fish, eating algae and organic detritus. The fossil record is scanty (Stewart, 2001), but reported from late Miocene deposits at Lothagam, Kenya (Stewart, 2003); Pliocene deposits in Wadi Natrun, Egypt (Greenwood, 1972), Koobi Fora, Kenya (Schwartz, 1983), the Lakes Albert and Edward Basins (Stewart, 1990); and Pleistocene deposits in the Western Rift (Van Neer, 1994). A reported Miocene occurrence from western Uganda may be in error; the author states that certain Mio–Pliocene sites had Pleistocene-aged fossils mixed in (Van Neer, 1994:90). *Labeo*-like teeth are also reported from the mid-Miocene of Loperot but are not confirmed (Van Couvering, 1977). In Lake Turkana, extant *Labeo* is represented by one species—*L. horie* Heckel, 1846. Elsewhere, the genus is widespread throughout the continent, including the Nile Basin, West Africa, eastern Africa, and the Congo and Zambezi Basins.

Barbus Cuvier and Cloquet, 1816

Barbus sp.

(Figures 5, 6)

KANAPOI MATERIAL. 3156, 4 teeth; 3845, 2 teeth; 3846, 3 teeth; 3849, 6 teeth.

Barbus is exclusively represented by its pharyngeal teeth (Figs. 5, 6), which represent small individuals, probably under 30 cm total length. These teeth do not resemble those of *B. bynni* Boulenger, 1911, the only similar sized *Barbus* now inhabiting Lake Turkana, but do resemble those of *B. altianalis* Boulenger, 1900; no other comparison with modern *Barbus* species was made. The teeth do not have the rows of small cusps observed on some *Barbus*? teeth recovered from Miocene deposits in Saudi Arabia (Otero and Gayet, 2001).

Like *Labeo, Barbus* is an inshore demersal (bottom-dwelling) fish, with a varied diet of ostracods, mollusks, insects, aquatic vegetation, and occasionally fishes. *Barbus* teeth are not common at Kanapoi, nor are they common at nearby Lothagam

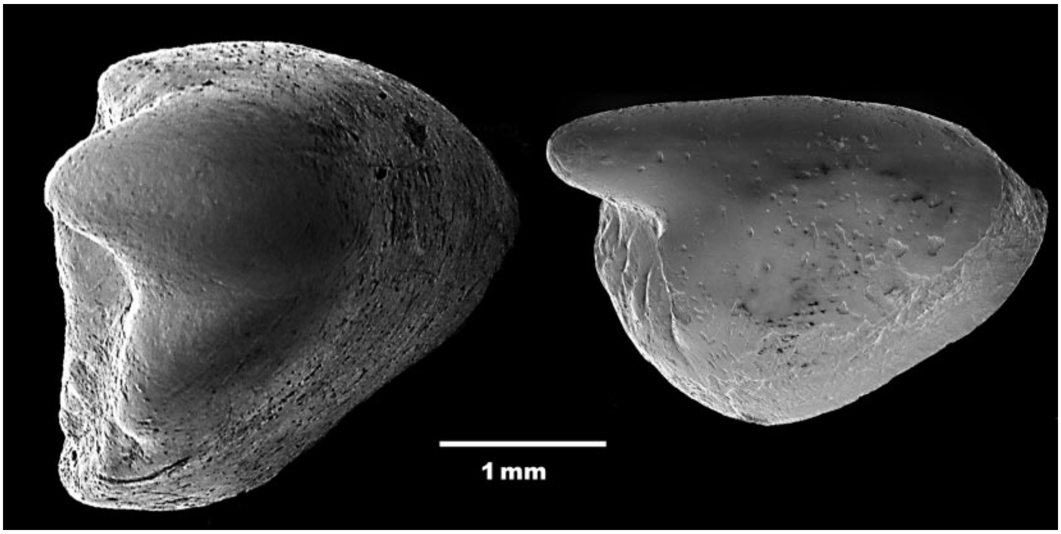

Figure 5 *Barbus* sp., SEM of pharyngeal tooth, ventral view (left) and side view (right), from Kanapoi

Figure 6 *Barbus* sp., SEM of pharyngeal tooth (different from Fig. 5), side view, from Kanapoi

(Stewart, 2003). Their fossil record in Africa is virtually nonexistent prior to the Pliocene (Stewart, 2001), with the earliest reported finds being from Pliocene deposits at Lothagam (Stewart, 2003), Pliocene deposits in the Western Rift, Congo (Stewart, 1990), Plio–Pleistocene deposits from Koobi Fora (Schwartz, 1983), and Pleistocene deposits from the Western Rift (Greenwood, 1959; Van Neer, 1994). Van Couvering (1977) notes that "*Barbus*-like" teeth are known from mid-Miocene deposits in Kenya. The report of a probable *Barbus* in Miocene deposits in Saudi Arabia (Otero, 2001; Otero and Gayet, 2001) indicates these fishes could have entered Africa from the Arabian region during land connections in the Burdigalian (early Miocene) (see discussion in Otero, 2001).

At present, *Barbus* is represented by three species in Lake Turkana, with only *B. bynni* attaining a length of at least 30 cm in Lake Turkana.

Order Characiformes

Family Distichodontidae

Distichodus Müller and Troschel, 1845

Distichodus sp.

(Figure 7)

KANAPOI MATERIAL. 3156, 1 tooth; 3845, 2 teeth; 3847, 2 teeth; 3849, 3 teeth.

Distichodus teeth are oral, lining the premaxilla and dentary (Fig. 7). The average height of the Kanapoi teeth was 5 mm long, which is within the size range of modern individuals.

Distichodus remains are not common at Kanapoi nor at Lothagam, but this may reflect their small size and probable poor preservation. The fossil record is poor (Stewart, 2001) but is known from Mio–Pliocene deposits in the Lakes Albert and Edward Basins (Van Neer, 1994), Pliocene deposits in the Lakes Albert and Edward Basins (Stewart, 1990), late Miocene deposits at Lothagam, Kenya (Stewart, 2003), and Pleistocene deposits at Koobi Fora (Schwartz, 1983). Extant *D. niloticus* (Linnaeus, 1762) is known from Lake Turkana and from the Nile Basin up to Lake Albert.

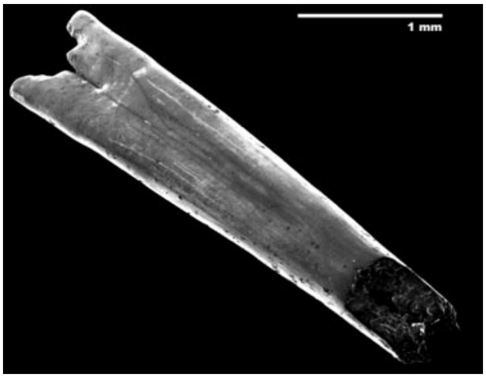

Figure 7 *Distichodus* sp., SEM of oral tooth, side view, from Kanapoi

Family Alestidae

Hydrocynus Cuvier, 1817

Hydrocynus sp.

(Figure 8)

KANAPOI MATERIAL. 3156, 23 teeth, 1 dentary fragment with tooth; 3845, 33 teeth, 1 dentary fragment with tooth; 3846, 3 teeth; 3847, 13 teeth, 1 dentary fragment with tooth, 1 premaxilla fragment; 3848, 32 teeth, 4 dentary fragments, 4 dentary fragments with teeth, 1 premaxilla fragment; 3849, 2 teeth.

Hydrocynus teeth are long and conical in shape (Fig. 8), with considerable size range. At Kanapoi, both teeth and jaw elements were recovered, often with the teeth in situ, usually in replacement sockets within the jaw element. Teeth and jaw elements

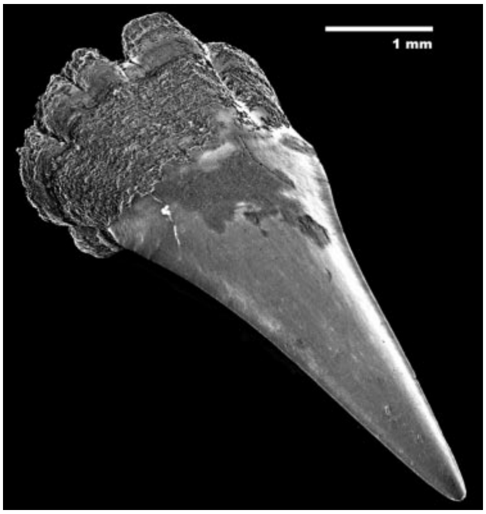

Figure 8 *Hydrocynus* sp., SEM of oral tooth and base, side view, from Kanapoi

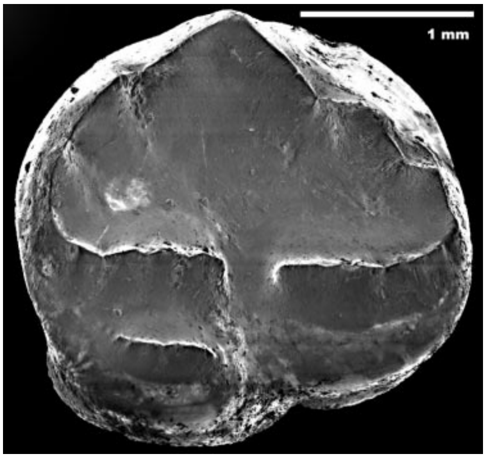

Figure 9 *Brycinus macrolepidotus*, SEM of second inner premaxillary tooth, occlusal view, from Kanapoi; labial side at bottom, lingual at top

represent individuals of up to 1 m in total length, although modern individuals in Lake Turkana do not exceed 65 cm in total length (Hopson and Hopson, 1982). Several small teeth with a broader base and more triangular shape than most teeth were determined, from modern *Hydrocynus* jaws, to be teeth which were just erupting.

The fossil record of *Hydrocynus* has been primarily based on teeth (Stewart, 2001); therefore, the recovery of jaw elements potentially provides new information about the fossil genus. *Hydrocynus* are pelagic and are voracious piscivores. Fossil *Hydrocynus* teeth are known from Mio–Pleistocene deposits in the Western Rift, Uganda (Van Neer, 1994), Miocene deposits of Sinda, Congo (Van Neer, 1992), late Mio–Pliocene deposits at Lothagam, Kenya (Stewart, 2003), Pliocene deposits in Wadi Natrun, Egypt (Greenwood, 1972), and the Western Rift, Congo (Stewart, 1990), and Plio–Pleistocene deposits in the Omo Valley (Arambourg, 1947) and at Koobi Fora (Schwartz, 1983). *Hydrocynus* is represented by one species, *H. forskalii* Cuvier, 1819, in Lake Turkana, but a second species, *H. vittatus* Castelnau, 1861, is present in the Omo River. *Hydrocynus* is widespread from Senegal to the Nile, including the Volta, Niger, and Chad Basins.

Brycinus Myers, 1929

B. macrolepidotus
(Cuvier and Valenciennes, 1849)

(Figures 9–11)

KANAPOI MATERIAL. 3156, 1 second inner premaxillary tooth.

Brycinus is represented only by a second inner premaxillary tooth (Fig. 9) which is identical to the

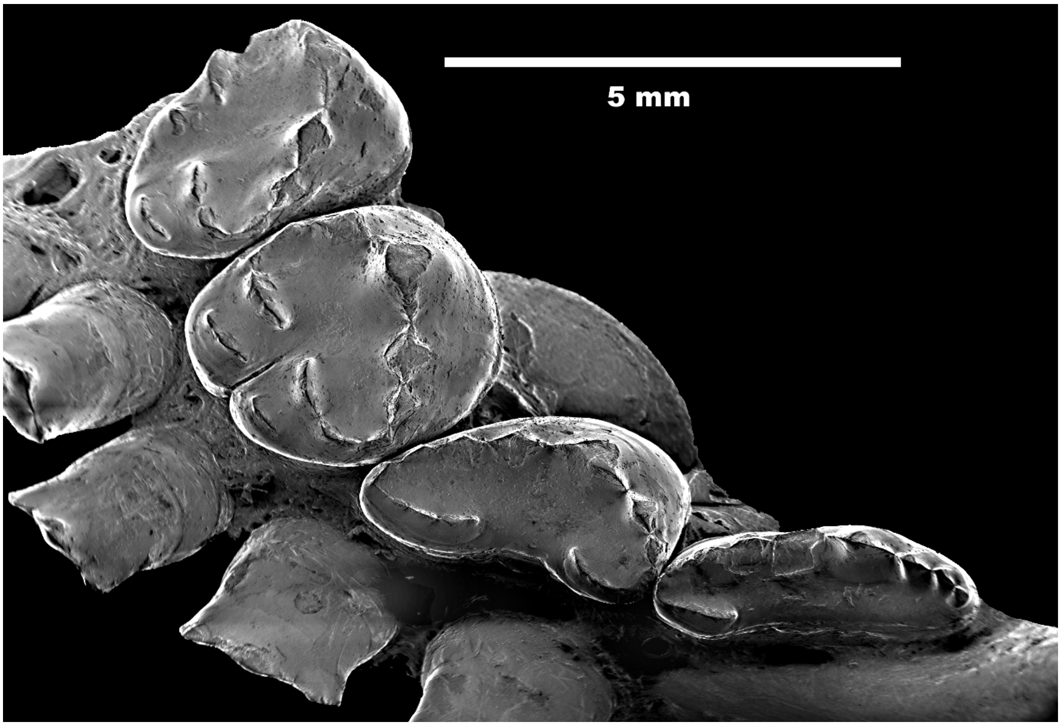

Figure 10 *Brycinus macrolepidotus*, SEM of first, second, third, and fourth inner premaxillary teeth (from left to right) and some outer teeth, occlusal views; lingual side at top right, labial at bottom left; modern specimen

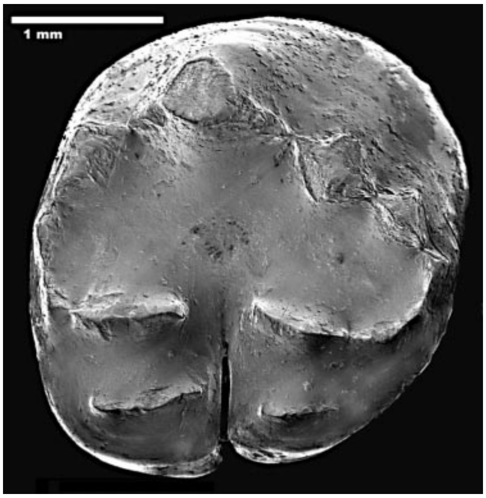

Figure 11 *Brycinus macrolepidotus*, SEM of second inner premaxillary tooth, occlusal view; labial side at bottom, lingual at top; modern specimen

same tooth in modern *B. macrolepidotus* specimens (Figs. 10, 11). *Brycinus macrolepidotus* has distinctive inner premaxillary teeth, which are not found in other alestid specimens. The tooth represents an individual of about 30 cm in total length.

A recent study has transferred *Alestes macrolepidotus* and twelve other *Alestes* Muller and Troschel 1844 species to the genus *Brycinus,* leaving five species in the genus *Alestes,* and five in a polyphyletic grouping referred to as "Brycinus" (Murray and Stewart, 2002). Both *Alestes* and *Brycinus* are genera within the Alestidae, which possess similar multicusped molariform teeth. In the following discussions, I will use "alestid" to refer to *Alestes* and/or *Brycinus,* but not to *Hydrocynus,* which is also alestid but with very different, conical teeth (see Murray and Stewart, 2002, for discussion of the terms Alestidae, "Hydrocyninae," and "Alestinae").

Use of fine-meshed screens at several sites resulted in recovery of many small cusped teeth, which in the field were thought to belong to *Alestes* or *Brycinus*. Closer inspection with a microscope revealed that these teeth actually belonged to *Sindacharax,* based on similarity to larger specimens (see discussion under *Sindacharax* Greenwood and Howes, 1975). The recovery of only one *Brycinus* tooth, particularly when fine-meshed screens (1-mm mesh) were used at several sites indicates the scarcity of this taxon at Kanapoi. *Brycinus* and *Alestes* were slightly more common at Lothagam.

The fossil record of *Brycinus* sp. (and *Alestes* sp.) is poor (Stewart, 2001), with remains known from Mio–Pliocene deposits at Lothagam, Kenya (Stewart, 2003), Plio–Pleistocene deposits in the Lakes Albert and Edward Basins (Stewart, 1990), Mio–Pleistocene deposits in the Western Rift (Van Neer, 1994), and Manonga, Tanzania (Stewart, 1997). Miocene teeth with alestid affinities are reported from Loperot and Mpesida, Kenya (Van Couvering, 1977). Modern alestids are represented by six species in Lake Turkana, including *A. baremoze* de Joannis, 1835; *A. dentex* Linnaeus, 1758; *B. nurse* Rüppell, 1832; *B. macrolepidotus; B. ferox* Hopson and Hopson, 1982; and *B. minutus* Hopson and Hopson, 1982. Modern alestids are found in the Volta, Niger, and Chad Basins to the Nile River, and in the Congo, Zambezi, and Limpopo Basins. Modern alestid species span a range of trophic adaptations and habitats. In modern Lake Turkana, they are generally pelagic and omnivorous.

Sindacharax Greenwood and Howes, 1975

A total of 2,272 teeth from Kanapoi are attributed to *Sindacharax*. This preponderance of *Sindacharax* teeth compared to numbers of elements of other fish reported here does not reflect actual abundance, but a selective collection policy.

Very few *Sindacharax* dentaries and/or premaxillae are known with in situ teeth, and none from Kanapoi, so identification of isolated teeth was accomplished by comparison with the complete dentary and premaxilla of *S. greenwoodi* Stewart, 1997, found at Lothagam (Stewart, 1997). However, because there is considerable individual variation in cusp patterns of teeth in known *Sindacharax* jaws, placement of these isolated teeth is tentative. Analysis of the in situ teeth and the isolated teeth at Lothagam indicated that outer premaxillary and dentary teeth were so similar among *Sindacharax* species, as were third and fourth inner premaxillary teeth, that no species designations for these teeth are made. As is the common convention, in this article, teeth are numbered sequentially, starting from the midline of the jaw (#1 left or right) and moving laterally.

As mentioned above in the discussion on modern alestids, many very small teeth (<2 mm) were recovered, which were initially thought to belong to *Brycinus* or *Alestes,* until closer examination indicated they were very small *S. mutetii* Stewart, 2003, and *S. lothagamensis* Stewart, 2003, teeth. The similarity in shape and cusping between small *Sindacharax* and modern alestid teeth leads to speculation on the development of the characteristic cusped ridges in *Sindacharax* teeth for which the genus is named (Greenwood and Howes, 1975; Greenwood, 1976). Examination of a range of *Sindacharax* inner premaxillary teeth indicates that, while the smaller teeth (ca. <2 mm) are cusped, in larger teeth, the cusps morph to form ridges. Once the ridges are formed, the tooth pattern remains consistent.

On the other hand, in several of the modern alestid specimens observed by the author (including *B. macrolepidotus, A. dentex, A. baremoze*), the inner teeth remained cusped in both large and small specimens, with one exception. Small *A. stuhlmanni*

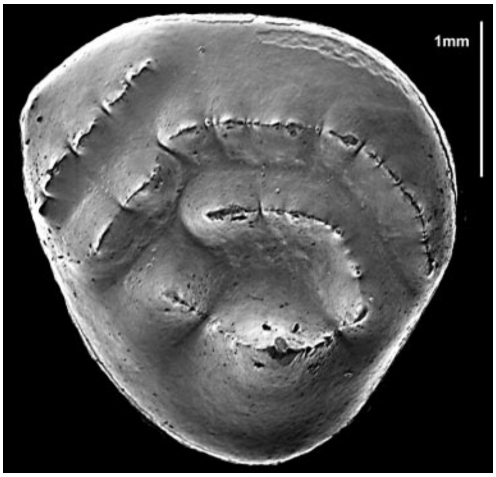

Figure 12 *Sindacharax lothagamensis*, SEM of second inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

Pfeffer, 1896, individuals had cusped teeth, but the larger specimens (ca. 24 cm in total length) had teeth with ridges (personal observation). Of particular interest therefore is whether teeth of other modern alestid species develop ridges after achieving a certain length and whether these teeth can be distinguished from *Sindacharax* teeth. This leads to some taxonomic difficulties, as the genus *Sindacharax* was erected based on its supposedly unique ridged teeth. While the analysis of existing *Sindacharax* jaw elements demonstrates enough differences with modern alestid elements to keep *Sindacharax* as a separate genus, the diagnosis of the *Sindacharax* genus needs to be re-examined in order to define it more accurately. However, more *Sindacharax* cranial and postcranial elements must be recovered for such revision.

Sindacharax lothagamensis Stewart, 2003

(Figures 12, 13)

KANAPOI MATERIAL. 3156, 2 second inner premaxillary teeth; 3848, 1 first inner premaxillary tooth; 3849, 17 first inner premaxillary teeth, 57 second inner premaxillary teeth; 29287, 7 first inner premaxillary teeth.

Teeth of *Sindacharax lothagamensis* are smaller on average than those of other *Sindacharax* and are relatively common at Kanapoi. The Kanapoi second inner premaxillary teeth are identical to both the holotype and the Isolated teeth found at Lothagam (e.g., Stewart, 2003: fig. 3.5) (Fig. 12). The size range of teeth differs slightly from that at Lothagam; at Lothagam, second inner premaxillary teeth ranged up to 5.5 mm in length with most under 3 mm, whereas the Kanapoi teeth ranged to 5 mm, with most under 2 mm. Numerous first inner teeth were found associated with the second inner teeth at Kanapoi, particularly at site 3849, and they showed a slightly different cusp pattern than that described for the Lothagam teeth (Stewart, 2003). These Kanapoi first teeth are long and narrow, with the dominant cusp at the lingual end of the tooth. A smaller cusp, not two, veers in a diagonal line towards the presumed bucco-labial side, and another cusp is positioned anterior to the dominant cusp. Anterior to this are one or more ridges traversing the width of the tooth (Fig. 13).

Figure 13 *Sindacharax lothagamensis*, SEM of first inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

Sindacharax lothagamensis teeth were the second most numerous of *Sindacharax* teeth at Kanapoi. This abundance of *S. lothagamensis* is a surprise, as they were primarily recovered in the late Miocene Lower Nawata deposits at Lothagam and only occasionally in later Pliocene deposits. Their abundance at Kanapoi suggests that absence in later Lothagam deposits may reflect a collection bias or different environmental conditions. Collection bias seems unlikely, as intensive collecting occurred at Pliocene deposits in Lothagam. However, different environmental conditions from the late Miocene to Pliocene deposits at Lothagam is certainly possible, with the latter providing unfavorable habitats for

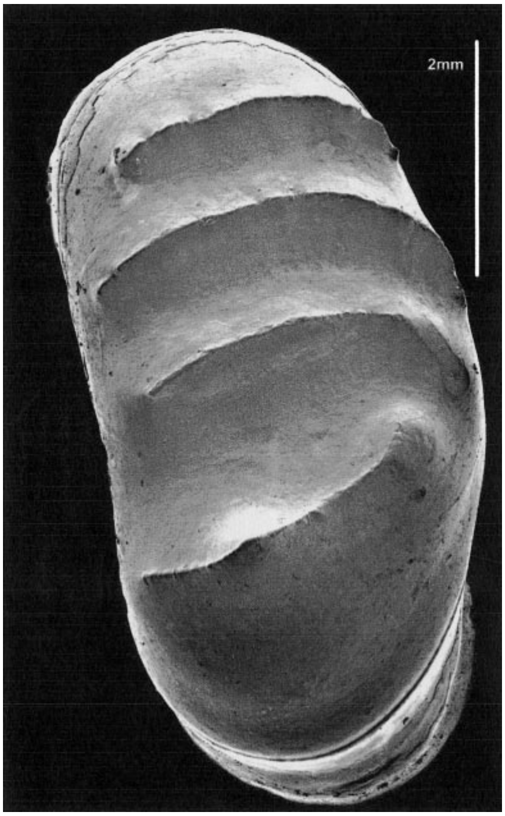

Figure 14 *Sindacharax mutetii*, SEM of first inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

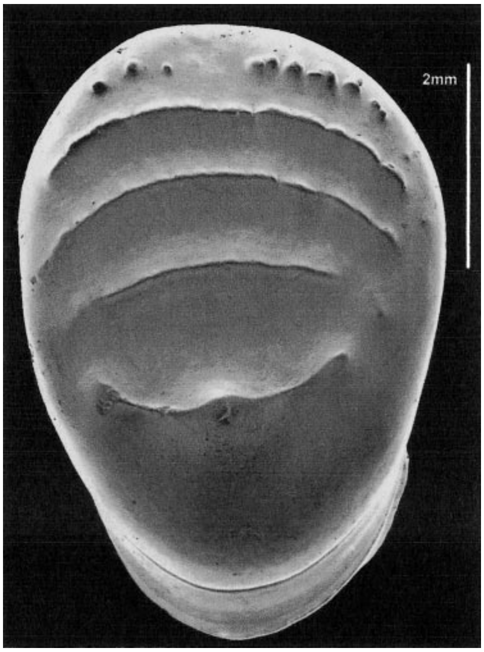

Figure 15 *Sindacharax mutetii*, SEM of second inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

S. lothagamensis, and Kanapoi may have provided a more favourable environment for them.

Sindacharax mutetii Stewart, 2003
(Figures 14–17)

EMENDED DIAGNOSIS. Second inner premaxillary tooth distinguished from *Sindacharax lepersonnei* Greenwood and Howes, 1975 and *S. lothagamensis* by cusps forming ridges rather than discrete cusps as in *S. lepersonnei* and *S. lothagamensis*. Distinguished from *S. deserti* Greenwood and Howes, 1975, by absence of raised circular ridge radiating from the dominant lingual cusp; distinguished from *S. greenwoodi* Stewart, 1997, by lack of the ridged arc surrounding dominant lingual cusp, and distinguished from all other *Sindacharax* by broad oval shape.

HOLOTYPE. A second inner premaxillary tooth, collected from Lothagam by Sam N. Muteti and Peter Kiptalam in 1993 from Site 1944 in the Apak Member of the Nachukui Formation, and now housed in the collections of the National Museums of Kenya, Nairobi, with the accession number KNM-LT 38265.

Figure 16 *Sindacharax mutetii*, SEM of second inner premaxillary tooth, occlusal view, from Kanapoi; labial side at top, lingual at bottom

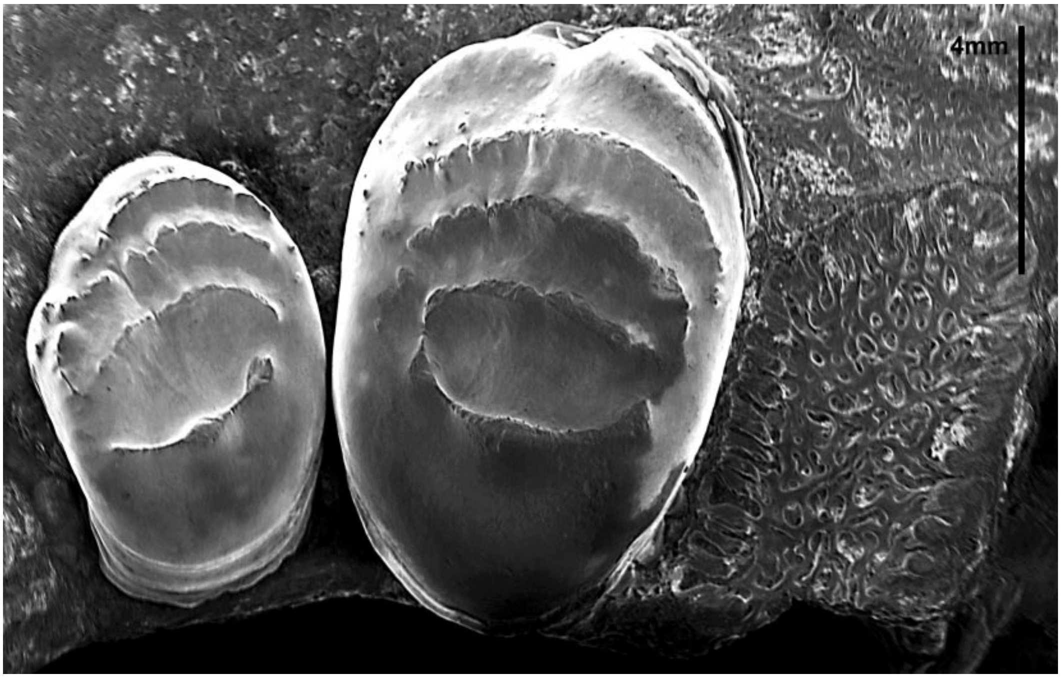

Figure 17 *Sindacharax mutetii*, SEM of in situ second and third inner premaxillary teeth, occlusal view, from Kanapoi; labial side at top, lingual at bottom, medial to the right, lateral to the left

KANAPOI MATERIAL. 3156, 3 second inner premaxillary teeth; 3845, 21 first inner premaxillary teeth, 26 second inner premaxillary teeth; 3846, 14 first inner premaxillary teeth, 39 second inner premaxillary teeth; 3847, 51 first inner premaxillary teeth, 75 second inner premaxillary teeth; 3848, 43 first inner premaxillary teeth, 67 second inner premaxillary teeth; 3849, 50 first inner premaxillary teeth, 73 second inner premaxillary teeth; ngui site, 28 first inner premaxillary teeth, 65 second inner premaxillary teeth.

Most first and second inner premaxillary teeth recovered were identical to those recovered from the Apak and Kaiyumung Members at Lothagam (Stewart, 2003) (Figs. 14, 15); however, a few second inner premaxillary teeth showed a slight deviation in cusp pattern (Fig. 16). Instead of the first ridge, which is anterior to the dominant cusp, traversing the whole width of the tooth, in some teeth it was shortened and often bracketed by one or both ends of the ridge anterior to it.

The large number of *S. mutetii* teeth recovered at Kanapoi reflect a range of individual variations in their cusp patterns. Several of the second and third inner premaxillary teeth recovered have similar patterns to their counterparts in situ on the premaxilla recovered from the Apak Member at Lothagam, which was ascribed to cf. *S. mutetii* (Stewart, 2003). Therefore, the Lothagam premaxilla is now included in *S. mutetii* (Fig. 17). This premaxilla remains the only jaw element recovered which is ascribed to *S. mutetii.*

A total of 555 teeth ascribed to *S. mutetii* were recovered at Kanapoi, making it the most abundant of the *Sindacharax* species at that site. *Sindacharax mutetii* teeth were also the most common teeth recovered from the Apak Member deposits at Lothagam, although this species was not recovered from the Murongori Member.

Stewart (2003) stated that *S. mutetii* was the only *Sindacharax* found at Kanapoi. However, further study of the Kanapoi specimens showed that, while *S. mutetii* is by far the most common species recovered, teeth of both *S. lothagamensis* and *S. howesi* Stewart, 2003, are also present.

Sindacharax howesi Stewart, 2003

KANAPOI MATERIAL. 3845, 3 first inner premaxillary teeth; 3846, 1 first inner premaxillary tooth; 3847, 8 first inner premaxillary teeth; 3848, 7 first inner premaxillary teeth, 2 second inner premaxillary teeth; 29287, 1 second inner premaxillary tooth.

Sindacharax howesi teeth were not common at Kanapoi. Mainly first inner premaxillary teeth were recovered, and these were identical to those found in the northern Kaiyumung deposits at Lothagam.

Sindacharax howesi teeth were exclusively found in the north Kaiyumung deposits at Lothagam, where they are numerous. Their appearance in the

Figure 18 *Sindacharax* sp., SEM of in situ third inner premaxillary tooth, from Kanapoi; labial side at top, lingual at bottom

Figure 19 *Sindacharax* sp., SEM of in situ fourth inner premaxillary tooth, from Kanapoi; labial side probably to the right, lingual probably to the left

Kanapoi deposits indicates a slightly earlier presence (ca. 4.0 Ma) in the Turkana Basin than previously thought.

Sindacharax sp.

(Figures 18, 19)

As discussed above, outer premaxillary and dentary teeth are indistinguishable between the species, and therefore are referred as *Sindacharax* sp. Similarly, third and fourth inner premaxillary teeth are similar among the species, and again were referred to *Sindacharax* sp.

Third and Fourth Inner Premaxillary Teeth

KANAPOI MATERIAL. 3845, 16 third or fourth inner premaxillary teeth; 3846, 11 third or fourth inner premaxillary teeth; 3847, 43 third inner premaxillary teeth, 15 fourth inner premaxillary teeth; 3848, 25 third or fourth inner premaxillary teeth; 3849, 32 third or fourth inner premaxillary teeth; 29287, 12 third or fourth inner premaxillary teeth.

No third or fourth inner premaxillary teeth could be assigned to species, as they were very similar throughout the deposits. Often the third and fourth teeth could not be distinguished from each other, as the only confirmed fourth premaxillary tooth (preserved in situ on the *S. greenwoodi* type specimen) is very worn and the cusp pattern almost indistinguishable. However, based on comparison with the *S. greenwoodi* premaxilla and modern *Alestes* and *Brycinus* premaxillae, I have tentatively assigned some teeth as third inner teeth (Fig. 18) and fourth inner teeth (Fig. 19).

Outer Teeth

While outer teeth are difficult to distinguish between species, there are several distinct types. Similar to the Lothagam outer teeth (Stewart, 2003a), I have classified the Kanapoi teeth into types, with an indication to which species they are most consisistently associated.

Outer Premaxillary Teeth, Type A

KANAPOI MATERIAL. 3156, 4 outer premaxillary teeth; 3845, 26 outer premaxillary teeth; 3846, 10 outer premaxillary teeth; 3847, 86 premaxillary outer teeth; 3848, 48 premaxillary outer teeth; 3849, 22 premaxillary outer teeth; 29287, 19 premaxillary outer teeth.

Type A teeth consist of one dominant and two much smaller flanking cusps, which slope into a short, uncusped platform on one side but have a steep shelf on the other side (see figs. 3.26 and 3.27

in Stewart, 2003). They have a round or oval attachment base. At Kanapoi, Type A teeth are associated with both *S. lothagamensis* and *S. mutetii* teeth; when associated with *S. mutetii,* they often have elongated attachment bases.

Outer Premaxillary Teeth, Type B

KANAPOI MATERIAL. 3845, 5 outer premaxillary teeth; 3846, 2 outer premaxillary teeth; 3847, 11 outer premaxillary teeth; 3848, 11 outer premaxillary teeth; 3849, 3 outer premaxillary teeth; 29287, 1 outer premaxillary tooth.

Type B teeth are similar to Type A but have one or more discrete cusps at the base of the platform (Stewart, 2003: figs. 3.26, 3.27). Their attachment base is round or a roundish oval. These teeth were most common in sites where *S. howesi* was also found.

Outer Premaxillary Teeth, Type C

KANAPOI MATERIAL. 3848, 5 outer premaxillary teeth.

Type C teeth have a dominant central cusp, flanked by concentric or semiconcentric rows of small cusps (Stewart, 1997: figs. 2, 3). Their attachment base is an elongated oval. These teeth were rare at Kanapoi, and no particular affiliation can be ascertained.

Outer Dentary Teeth

The outer dentary teeth recovered were mainly first, second, and third teeth; fourth teeth are much smaller and fewer have been recovered. The first tooth is usually truncated posteriorly, to accommodate the inner tooth. There is considerable wear visible on most dentary teeth, and it is often difficult to describe any morphology on the teeth. As with premaxillary outer teeth, outer dentary teeth can be divided into types, although only Type A was recovered at Kanapoi.

Outer Dentary Teeth, Type A

KANAPOI MATERIAL. 3156, 5 outer dentary teeth; 3845, 85 outer dentary teeth; 3846, 61 outer dentary teeth; 3847, 205 outer dentary teeth; 3848, 134 outer dentary teeth; 3849, 295 outer dentary teeth; 29287, 122 outer dentary teeth.

All dentary teeth recovered at Kanapoi belonged to Type A, although many were too worn to ascertain type. These teeth have a dominant, pointed cusp and are flanked by two smaller cusps, which form a shelf on one side, more elongated and less steep than that of the premaxillary teeth (illustrated in Stewart, 2003). On the other side, the cusps slope into a broad platform, which is usually uncusped but may be weakly cusped. The attachment base is much more elongated than in most premaxillary teeth. Outer dentary teeth were by far the most abundant of all *Sindacharax* teeth, probably because of their size and robust attachment bases.

Inner Dentary Teeth

KANAPOI MATERIAL. 3845, 8 inner dentary teeth; 3846, 4 inner dentary teeth; 3847, 22 inner dentary teeth; 3848, 7 inner dentary teeth; 3849, 5 inner dentary teeth; 29287, 5 inner dentary teeth.

These teeth are very similar in both *Alestes* and *Sindacharax*. There is only one inner tooth on each dentary in living individuals, and it is positioned posterior to a notch in the first outer dentary tooth. Inner dentary teeth are small and round in shape, with a single elongated centrally placed cusp.

Worn and/or Fragmented Teeth, Unassigned to Position

KANAPOI MATERIAL. 3156, 1 tooth; 3845, 6 teeth; 3846, 48 teeth; 3847, 85 teeth; 3848, 50 teeth; 3849, 4 teeth; 29287, 50 teeth.

Order Siluriformes

Family Bagridae or Family Claroteidae

KANAPOI MATERIAL. 3156, 1 pectoral spine fragment; 3847, 1 cranial spine.

These catfish elements are referred to the family level both because of their incomplete nature and the similarity of these elements between some bagrid and claroteid species. They represent small individuals, probably no longer than 50 cm in total length.

Bagrid and/or claroteid catfish elements were common in the field at Kanapoi, often representing large individuals (approximately 1 m in length). Most of these elements were not collected. Many of these appeared to belong to *Clarotes* Kner, 1855, a large catfish which today often inhabits deltaic regions. Bagrids and claroteids, particularly *Bagrus* Bosc, 1816, and *Clarotes*, are known from the Mio–Pliocene deposits at Lothagam (Stewart, 2003) and at Koobi Fora (Schwartz, 1983), as well as other Cenozoic deposits in Africa. They do not appear to have radiated in the Turkana Basin as they did in the Western Rift (Stewart, 2001), although they are more common in the Plio–Pleistocene deposits at eastern Turkana.

Family Clariidae

Clarias Scopoli, 1777

Heterobranchus Geoffroy Saint-Hilaire, 1809

Clarias sp. or *Heterobranchus* sp.

KANAPOI MATERIAL. 3847, 2 caudal vertebrae; 3849, 2 trunk vertebrae, 1 caudal vertebrae.

These vertebrae are referred to *Clarias* or *Heterobranchus* because of great similarity between the elements. These vertebrae derive from small individuals (<50 cm total length).

Clariid elements were abundant at Kanapoi, but not collected. As with the bagrid catfish, many elements appeared to come from large individuals, up to 2 m in length. *Clarias* is a bottom-dwelling, in-

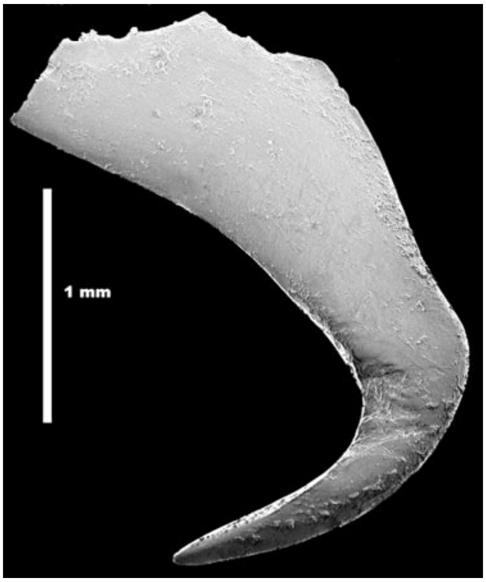

Figure 20 *Synodontis* sp., SEM of dentary tooth, from Kanapoi; side view

shore fish, which can tolerate highly deoxygenated waters. Clariid remains were common throughout the Lothagam deposits (Stewart, 2003) and in late Cenozoic deposits of Africa (Stewart, 2001). Tentative identifications are reported in the mid-Miocene from Bled ed Douarah, Tunisia (Greenwood, 1973), and Ngorora, Kenya (Schwartz, 1983). Definite clariid remains are known from Miocene deposits in Sinda, Congo (Van Neer, 1992), and Chalouf, Egypt (Priem, 1914); Mio–Pliocene deposits in Manonga, Tanzania (Stewart, 1997); Mio–Pleistocene deposits in the Western Rift (Van Neer, 1994); Pliocene deposits in Wadi Natrun, Egypt (Greenwood, 1972); and Plio–Pleistocene deposits at Koobi Fora (Schwartz, 1983). Extant *Clarias* is represented by *C. lazera* Cuvier and Valenciennes, 1840, in Lake Turkana. *Clarias* is widespread throughout Africa, including the Nile, Congo, and Zambezi Basins.

Heterobranchus has a similar appearance and size to *Clarias,* but may be more sensitive to high salinity values. Modern *H. longifilis* Valenciennes, 1840, is present in Lake Turkana, but is rare. Like *Clarias, Heterobranchus* is widespread throughout the major river basins of Africa. It was identified in late Pleistocene Lake Edward Basin (Congo) deposits (Greenwood, 1959).

Family Mochokidae

Synodontis Cuvier, 1817

Synodontis sp.

(Figures 20, 21)

KANAPOI MATERIAL. 3845, 5 teeth; 3847, 1 cranial spine base.

Synodontis teeth were not common in the Kanapoi sites sampled, suggesting *Synodontis* was not a dominant presence at Kanapoi. The teeth are located on the dentary and are curved (Fig. 20). They averaged about 1 mm in width, similar to modern *Synodontis* in Lake Turkana, suggesting the fossil fish reached 30–35 cm in total length (and much larger than the other Lake Turkana mochokid, *Mochocus* de Joannis, 1935, which reaches only 6.5 cm in length). The cranial spine base recovered is fragmentary (Fig. 21) but very similar to that of modern *Synodontis.* In life, it is positioned anterior to the dorsal cranial spine and resembles a truncation of the spine.

Synodontis was probably not common at Kanapoi, as its remains normally preserve well. It was also not common at Lothagam, although consistently present through the deposits. *Synodontis* inhabits all zones of lakes and rivers, and is omnivorous, eating insects, small fish, mollusks, and zooplankton. Fossil *Synodontis* is also known from Miocene deposits at Rusinga and Chianda, Kenya (Greenwood, 1951; Van Couvering, 1977), Moghara and Chalouf, Egypt (Priem, 1920), and Bled ed Douarah, Tunisia (Greenwood, 1973); Mio–Pleistocene deposits in the Western Rift (Greenwood and Howes, 1975; Van Neer, 1992, 1994); Pliocene deposits in the Western Rift (Stewart, 1990) and Wadi Natrun (Greenwood, 1972); and Plio–Pleistocene deposits at Koobi Fora (Schwartz, 1983). Two species of *Synodontis* inhabit modern Lake Turkana—*S. schall* Bloch and Schneider, 1801, and *S. frontosus* Vaillant, 1895. *Synodontis* is also widespread in systems throughout the African continent.

Order Perciformes

Suborder Percoidei

Family Latidae

Lates Cuvier, *in* Cuvier and Valenciennes, 1828

Lates niloticus (Linnaeus, 1758)

KANAPOI MATERIAL. 3845, 1 hyomandibular, 1 premaxilla, 1 dentary, 1 first trunk vertebra, 2 trunk vertebrae, 1 caudal vertebra; 3847, 2 premaxillae, 2 posttemporal, 1 quadrate, 1 articular, 1 basioccipital fragment, 1 vomer, 6 first trunk vertebra, 1 trunk vertebra; 3848, 1 basioccipital, 1 premaxilla, 1 vomer.

These elements are identical to those in modern *Lates niloticus* and represent fish of a diverse size range. Several large fossil elements were compared with modern *L. niloticus* elements recovered from the lake margin, and these indicated that many of the Kanapoi fish had an estimated total length of over 2 m.

Many elements of *Lates niloticus* were observed in the field at Kanapoi, but only those listed above were collected, for their diagnostic value. Many of

Figure 21 *Synodontis* sp., SEM of cranial spine base, from Kanapoi, ventral view

the bones represented large individuals, estimated to be approximately 2 m in length. Clearly, *L. niloticus* was a common component of the Kanapoi fish fauna, and with many large individuals must have been one of the most voracious consumers of fish in the aquatic food chain. Modern *Lates* inhabits most zones of lakes and rivers, although it only tolerates well-oxygenated waters. It is highly piscivorous.

Elements of fossil *Lates* spp. are common in African deposits (Stewart, 2001) and are known from Miocene deposits from Rusinga, Kenya (Greenwood, 1951), Gebel Zelten and Cyrenaica, Libya, (Arambourg and Magnier, 1961), Moghara and Chalouf, Egypt (Priem, 1920), Bled ed Douarah, Tunisia (Greenwood, 1973); Mio–Pliocene deposits at Lothagam, Kenya (Stewart, 2003); Plio–Pleistocene deposits from Lakes Albert and Edward Basins (together with *Semlikiichthys rhachirhinchus*) (Greenwood, 1959; Greenwood and Howes, 1975; Stewart, 1990; Van Neer, 1994); an unpublished report from Marsabit Road, Kenya (in Schwartz, 1983), the lower Omo Valley (Arambourg, 1947), and Koobi Fora (Schwartz, 1983); and Pliocene deposits from Manonga, Tanzania (Stewart, 1997), and Wadi Natrun, Egypt (Greenwood, 1972). *Lates niloticus* has also been reported from Messinian (late Miocene) deposits in Italy, the only confirmed report of this species in Europe (Otero and Sorbini, 1999). Elements formerly identified as *Lates* from Eocene deposits in Fayum, Egypt (Weiler, 1929), were referred to *Weilerichthys fajumensis* (Otero and Gayet, 1999b). Modern *Lates* is known from Lake Turkana (*L. niloticus* and *L. longispinis* Worthington, 1932) and is widespread throughout northern, eastern, and western Africa from Senegal to and including the Nile and Congo River Basins.

Percoidei incertae sedis

Semlikiichthys Otero and Gayet, 1999

Semlikiichthys rhachirhinchus (Greenwood and Howes, 1975)

Semlikiichthys cf. *S. rhachirhinchus*

KANAPOI MATERIAL. 3845, 4 first trunk vertebrae, 16 trunk vertebrae, 2 caudal vertebrae; 3846, 1 dentary, 1 first trunk vertebra, 5 trunk vertebrae, 4 caudal vertebrae; 3847, 4 dentaries, 1 first trunk vertebra, 9 trunk vertebrae, 3 caudal vertebrae; 3848, 1 vomer, 2 basioccipital, 4 first trunk vertebrae.

All material collected at Kanapoi is identical to drawings of *Semlikiichthys rhachirhinchus* (formerly *Lates rhachirhinchus* [Greenwood and Howes 1975] but renamed *S. rhachirhynchus* [Otero and Gayet, 1999a]; this author adheres to the original spelling [Greenwood and Howes, 1975] for “rhachirhinchus”), and is also identical to material collected at Lothagam, figured and described as *Semlikiichthys* cf. *S. rhachirhinchus* (Stewart, 2003). Full descriptions and photos of the extensive *Semlikiichthys* cf. *S. rhachirhinchus* material from Lothagam are found in the Lothagam volume (Stewart, 2003), where it is compared with the original drawings of *L. rhachirhinchus* (Greenwood and Howes, 1975).

In particular, the vomer recovered from Kanapoi is fully described in the Lothagam volume (Stewart, 2003), as it is the only vomer recovered from either Kanapoi or Lothagam which is almost identical to the type *S. rhachirhinchus* vomer (Greenwood and Howes, 1975), and is important in the naming of these fossils (*rhachirhinchus* means loosely “snout with spine”).

The Kanapoi elements establish a strong presence of *Semlikiichthys* cf. *S. rhachirhinchus* at Kanapoi.

As at Lothagam, *Lates niloticus* and *Semlikiichthys* cf. *S. rhachirhinchus* appear to have coexisted at Kanapoi. Both groups of fish seem to have attained large size, up to 2 m in length. This author has previously suggested (Stewart, 2001, 2003) that the presence of *Semlikiichthys* in the Turkana Basin resulted from exchange of faunas with the Lakes Albert and Edward Basins, the only other basins in which *Semlikiichthys* is known. Its reasonably common presence in Kanapoi further supports the suggestion of exchange. The identification of a palatine in Wadi Natrun Pliocene deposits probably referable to *Semlikiichthys* (Greenwood, 1972; Greenwood and Howes, 1975; discussed in Stewart 2001, 2003) also supports a more widespread faunal exchange within the Nile-linked systems, extending to the Egyptian Nile area.

Lates or *Semlikiichthys*

KANAPOI MATERIAL. 3156, 3 first trunk vertebrae, 1 caudal vertebra; 3845, 1 dorsal spine; 3846, 1 trunk vertebra; 3847, 1 maxilla fragment, 1 basioccipital, 1 pelvic spine; 3848, 1 basioccipital fragment, 4 vertebra fragments.

Perciformes Indeterminate

KANAPOI MATERIAL. 3156, 5 pelvic spines.

Pelvic spines are often difficult to distinguish between cichlids and *Lates/Semlikiichthys*. One pelvic spine appears to be more similar to those of cichlids, but not enough for positive identification. If so, it would be the only cichlid fossil recovered at Kanapoi. Cichlids are similarly rare at Lothagam.

PALEOECOLOGY

The Kanapoi fish fauna is characterized by two trophic components: large, piscivorous fish, in particular the polypterids, *Gymnarchus, Hydrocynus, Lates* (and probably *Semlikiichthys* by analogy), and the bagrid and clariid catfish; and medium to large molluscivores, including *Hyperopisus, Gymnarchus* (which is also a piscivore), *Sindacharax,* and possibly *Labeo*. Together with the numerous elements of the crocodile *Euthecodon* Fourteau, 1920, identified in the Kanapoi deposits, there was clearly much piscivory in this region of the Lonyumun lake (see, e.g., Tchernov, 1986, for details of *Euthecodon*). While *Euthecodon*'s diet probably consisted of the plethora of fish in the lake, the diet of the piscivorous fish must have included the numerous *Sindacharax, Hyperopisus,* and *Labeo* individuals, as well as smaller fish whose elements were not preserved. The near-absence of herbivorous fish, including *Barbus, Alestes,* and the large tilapiine cichlids is surprising. Most of these groups are common in modern Lake Turkana and the Nile system, and would be expected in the Pliocene lake. Certain absences may be explained by unfavorable environmental conditions (see **DISCUSSION AND SUMMARY** section). *Barbus* and the large tilapiine cichlids are generally scarce in African fossil deposits prior to the Pleistocene (Stewart, 2001).

The diversity and composition of taxa represented at Kanapoi is reminiscent of the modern Omo River Delta in northern Lake Turkana, which is inhabited, among other fish, by mormyriforms, characoids, bagrids, claroteids, and percoids. *Gymnarchus* and *Clarotes* in particular prefer delta regions (Lowe-McConnell, 1987). Many of the fish in the modern Omo River Delta region are intolerant of saline waters and therefore inhabit the delta and the lower reaches of the Omo River because they cannot tolerate the more saline Lake Turkana waters. Modern *Lates* is intolerant of deoxygenated waters, and the modern mormyriforms are intolerant of saline waters. By analogy with the modern Omo River Delta, Kanapoi waters may also therefore have been well-oxygenated and fresh.

The scarcity of fish such as *Protopterus, Polypterus* Saint-Hilaire, 1802, and *Heterotis* Ruppell, 1829, which were relatively common in the Nawata Formation at Lothagam, may signify an absence of vegetated, shallow backwaters or bays, as these are the type of habitats frequented by modern members of these taxa. The nearby Pliocene site of Eshoa Kakurongori contained numerous *Protopterus* toothplates, indicating a very different environment from Kanapoi.

DISCUSSION AND SUMMARY

Because the Kanapoi fish fauna comes primarily from one phase in the Kanapoi Formation—the lacustrine phase—there are no evolutionary or environmental transitions documented as was apparent through the Nawata and Nachukui Formations at the nearby Lothagam site. Nevertheless, the fauna alters some of the evolutionary and biogeographic interpretations made from the Lothagam fauna, as discussed below.

Most surprising is the comparison of the taxonomic composition from the Lothagam Muruongori deposits, Kanapoi deposits, and what the author has observed from the Ekora site deposits, all of which are presumed to derive from the Lonyumun Lake. The Muruongori deposits contain similar taxa to that at Kanapoi (Table 1), but also include two *Sindacharax* taxa—*S. deserti* and *S. greenwoodi*—and two *Tetraodon* Linnaeus, 1758, taxa—*T. fahaka* Hasselquist, 1757, and *Tetraodon* sp. nov., Stewart, 2003—which are common at Muruongori and at Ekora but which are completely absent from Kanapoi. Further, the most common *Sindacharax* species at Kanapoi—*S. mutetii*—is absent in the Muruongori Member and apparently in the Ekora fauna, although common in the Apak Member of Lothagam.

There are several possible explanations for this disparity in taxa between Kanapoi on one hand and Muruongori and Ekora on the other, which derive from the same lake. First, the different sites may represent different time intervals in the lake's history: the Ekora tetrapod fauna is said to be younger than that at Kanapoi (Maglio in Behrensmeyer, 1976), and the Muruongori Member may also be slightly younger than at Kanapoi. The "new" *Sindacharax* and *Tetraodon* taxa from Muruongori and Ekora may represent immigrants from a new inflow which was not present during Kanapoi deposition. The abundance of *S. mutetii* at both Kanapoi and in the Apak Member of Lothagam, which dates earlier than Muruongori and Ekora, may suggest an earlier deposition of the Kanapoi deposits, and a faunistic change between the Kanapoi, and Muruongori and Ekora waters. *Sindacharax mutetii* is completely absent from Muruongori and Ekora.

Alternatively, the Kanapoi and Muruongori and

Table 1 Fish taxa found in Mio–Pliocene deposits in Nawata, Apak, Muruongori, and Kaiyumung Members, Lothagam (Stewart, 2003) and Kanapoi (this report); see Feibel (2003a) and McDougall and Feibel (1999) for detailed information about the geochronology, geological formations, and members at Lothagam

	Nawata	Apak	Muruongori	Kaiyumung	Kanapoi
Protopterus sp.	+	+		+	
Polypterus sp.	+	+	+	+	+
Heterotis sp.	+	+	+		
Hyperopisus sp.		+	+	+	+
Gymnarchus sp.	+	+	+	+	+
Labeo sp.	?+	+	+	+	+
Barbus sp.		+		+	+
Distichodus sp.	+	+			+
Hydrocynus sp.	+	+	+	+	+
Brycinus macrolepidotus					+
Alestidae sp.	+			+	
Sindacharax lothagamensis	+	+			+
S. mutetii		+		+	+
S. howesi				+	+
S. deserti			+	+	
S. greenwoodi			+	+	
Sindacharax sp.	+	+	+	+	+
Bagrus sp.				+	
Aff. *Bagrus* sp.	+	+		+	
Clarotes sp.	+	+		+	
Bagridae/Claroteidae					+
Schilbe sp.	+				
Clarias or *Heterobranchus*	+	+		+	+
Synodontis sp.	+	+	+	+	+
Lates niloticus	+	+		+	+
Lates sp.	+	+	+	+	+
Semlikiichthys cf. *S. rhachirhinchus*	+	+	+	+	+
Cichlidae			+	+	
Tetraodon sp. nov.			+		
Tetraodon sp.			+	+	

Ekora deposits may represent different ecological zones in the Lonyumun Lake, with the "new" taxa restricted ecologically to local habitats and/or basins. Again the analogue of the modern Omo River Delta is appropriate here, with many taxa restricted to the delta region and not occurring in Lake Turkana proper.

A third alternative is that the field sampling was not extensive enough, and elements of the "new" taxa were not recovered at Kanapoi. This alternative seems less likely, as extensive screening was undertaken at all areas, and teeth of the "new" taxa should at least be somewhat represented at Kanapoi. Further, the *Tetraodon* toothplates are very robust and distinctive as fossils, and extensive surveying at Kanapoi should have recovered at least some toothplates, if this taxon had been present.

A third "new" taxon—cf. *Semlikiichthys rhachirhinchus*—was rare in earlier Lothagam deposits, but was common in the Muruongori Member at Lothagam, at Kanapoi, and at Ekora. This percoid apparently coexisted with *Lates niloticus,* which was also recovered in large numbers. Stewart (2001) has reported that *S. rhachirhinchus* elements were also found in the Western Rift and probably at Wadi Natrun, suggesting interchange between the three systems. Otero and Sorbini (1999) have suggested that the genus *Lates* diversified in the fresh waters of Europe and Africa in the Miocene, from a Mediterranean origin. Further work is needed to clarify the relationships of *S. rhachirhinchus*.

In sum, the Kanapoi fauna is of considerable interest for several reasons. It has an unusual composition of mainly large piscivorous fish and medium to large molluscivores, and a scarcity of herbivorous fish. This composition is considerably different from that of modern Lake Turkana, which is much more evenly balanced between herbivores and piscivores. The scarcity of herbivores such as *Barbus* and the large tilapiine cichlids, common in the modern lake and the Nile River system, is particularly enigmatic.

While the Kanapoi fauna shares many taxa with the similarly aged Muruongori Member fauna from Lothagam and also from Ekora, it also shows some differences. The dominance of *Sindacharax mutetii* at Kanapoi and in the Apak Member at Lothagam contrasts with its absence in the Muruongori deposits and at Ekora, as does the dominance of *S. deserti* and *Tetraodon* at Muruongori and Ekora, and their absence from Kanapoi and the Apak Member. Whether these disparities reflect ecological variants or chronological differences needs to be further studied.

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EARLY PLIOCENE TETRAPOD REMAINS FROM KANAPOI, LAKE TURKANA BASIN, KENYA

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APPENDIX BY ALISA J. WINKLER[4]

ABSTRACT. Kanapoi, located in the southwestern portion of the Lake Turkana Basin, is the type locality of the oldest East African australopithecine species, *Australopithecus anamensis,* and has yielded a diverse tetrapod assemblage that includes more than 50 species. The terrestrial fossils derive from fluviatile sands that date between 4.17 and 4.07 Ma and which sandwich a lacustrine interval that represents the extensive Lonyumun Lake—a predecessor of Lake Turkana. The tetrapod assemblage is broadly similar to comparably aged assemblages from the nearby locality of Lothagam and the slightly older site of Aramis in Ethiopia. Soil horizons from the succession suggest a mixture of habitats similar to those in the vicinity of the Omo Delta at the north end of the modern Lake Turkana. The Kanapoi biota, however, appears to represent a mixture of open and closed xeric habitats.

INTRODUCTION

The early Pliocene locality of Kanapoi is located to the southwest of Lake Turkana in northern Kenya at 36°3′51.1″E, 2°18′32.2″N. The Kanapoi sites were first collected in the mid-1960s (1965–67) by expeditions from Harvard University under the leadership of Bryan Patterson. Significant among the 400 specimens collected by the Harvard University parties are the holotypes of the elephantid *Loxodonta adaurora* Maglio, 1970, and rhinocerotid *Ceratotherium praecox* Hooijer and Patterson, 1972, two of the most characteristic components of the East African Pliocene biota, together with a hominid humerus that was tentatively identified as *Australopithecus* sp. (Patterson et al., 1970). Some elements of the fauna were described in detail, including proboscideans (Maglio, 1970, 1973), suids (Cooke and Ewer, 1972), and rhinos (Hooijer and Patterson, 1972), but the remainder of the material was largely overlooked.

Kanapoi was subsequently recollected in the mid-1990s by National Museums of Kenya expeditions under the leadership of Meave Leakey. The vertebrate fauna was considerably augmented and the hominid hypodigm was expanded to include cranial, dental, and postcranial material of *Australopithecus anamensis* Leakey et al., 1995, currently the oldest recognized East African australopithecine (Ward et al., 2001). The age of the Kanapoi biota is tightly constrained to between 4.17 and 4.07 Ma (Leakey et al., 1998) and, as such, it documents a perilacustrine assemblage from an interval of time that is not well represented elsewhere in the Lake Turkana Basin.

We provide here a description of much of the fossil vertebrate material recovered by the Harvard University and National Museums of Kenya expeditions. The fish and carnivorans are described separately by Kathy Stewart and Lars Werdelin, respectively, in adjacent parts of this *Contributions in Science* issue, as is an assessment of the geologic context by Craig Feibel. The micromammals will be investigated by Frederick Kyalo of the National Museums of Kenya for his Ph.D. dissertation, but a preliminary assessment of this material by Alisa Winkler is appended to this contribution.

GEOLOGIC SETTING

The stratigraphic sequence at Kanapoi reflects deposition in fluviatile and lacustrine environments and has been studied by Denis Powers (1980) and Craig Feibel (2003b). A basal fluvial complex of channel sandstones and floodplain paleosols lies on the dissected surface of Miocene volcanic rocks. Two devitrified tuffs in this lower fluviatile unit have yielded dates of 4.17 ± 0.03 Ma (lower pumiceous tuff) and 4.12 ± 0.02 Ma (upper pumiceous tuff) (Leakey et al., 1995). In this unit, vertebrate fossils occur primarily in the vertic floodplain paleosols. The basal complex is overlain by claystones with ostracods and mollusks; these were deposited within the early Pliocene Lonyumun Lake that extended throughout much of the Lake Turkana Basin. The vitric Kanapoi Tuff from the upper portion of the lower lacustrine sequence con-

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tained pumices that were dated to 4.07 ± 0.02 Ma (Leakey et al., 1998). This tuff cannot be matched with any tephra exposed in the northern part of the Lake Turkana Basin but shows affinity with tephra from the Lake Baringo Basin. The lacustrine strata are overlain by extensive deltaic sandstones that are rich in vertebrate remains, and these are in turn overlain by a second fluvial interval that has extensive conglomeratic channels near its top. The sequence is capped by the Kalokwanya Basalt that has been dated to 3.4 Ma, providing an upper limit on the age of the formation (Feibel, 2003b).

CONVENTIONS AND ABBREVIATIONS

The full accession number for Kanapoi specimens housed at the National Museums of Kenya in Nairobi begins with the prefix KNM-KP (e.g., KNM-KP 435). This prefix is abbreviated to KP in the descriptive portions of the text and omitted altogether in the list of Kanapoi material at the beginning of each systematic section. The following abbreviations appear in the lists of specimens and in the tables:

ant = anterior
ap = anteroposterior
BL = buccolingual
dist = distal
EK = Ekora
frag = fragment
h/c = horn core
juv = juvenile
KP = Kanapoi
LL = labiolingual
LT = Lothagam
Lt = left
lt = length
MD = mesiodistal
mand = mandible
max = maxilla
met = width at metaloph(id)
m/p = metapodial
m/t = metatarsal
PL = plastron length
post = posterior
prot = width at protoloph(id)
prox = proximal
p/c = postcranial
Rt = right
tr = transverse

SYSTEMATIC DESCRIPTION

Order Chelonia

Family Pelomedusidae

Turkanemys Wood, 2003

Turkanemys pattersoni Wood, 2003

KANAPOI MATERIAL. 435, carapace; 436, carapace; 437, carapace frags; 451, carapace frags; 562, partial carapace and plastron; 30174, carapace and plastron; 30438, carapace and plastron; 30470, carapace and plastron; 30595, carapace; 30597, carapace and plastron; 30618, carapace and plastron.

Turkanemys pattersoni was recently described from Lothagam (Wood, 2003). Its shell differs from all other African pelomedusid species by virtue of having trapezoidally shaped first vertebral scute and in the tendency of the nuchal bone to be proportionally broader than in other species. The shell differs from all South American species of *Podocnemis* (to which many African fossil pelomedusids have been referred in the past as a matter of convenience) in having six rather than seven neural bones and a triangular rather than pentagonal intergular with gulars meeting in the midline behind it. *Turkanemys pattersoni* also differs from all other pelomedusid species in the structure of the cervical series, with articular surfaces being intermediate in shape between saddle joints of typical podocnemines and procoelous condition of pelomedusines and *Erymnochelys madagascariensis* Grandier, 1867. *Turkanemys pattersoni* is the most common chelonian from Kanapoi.

Kenyemys Wood, 1983

Kenyemys sp. indet.

KANAPOI MATERIAL. 30419, carapace frags; 30468, juvenile carapace and plastron.

Kenyemys williamsi Wood, 1983, differs from all other known pelomedusids by the following combination of characters: (a) a series of elongate tuberosities forming an interrupted keel extending along the midline rearward from the dorsal surface of the second neural bone; (b) six neural bones forming a continuous series, the anterior end of the first abutting directly against the rear margin of the nuchal bone and the sixth one being heptagonal; (c) outer corners of nuchal bone extending beyond lateral margins of first vertebral scute; (d) pentagonal shape of first vertebral scute; (e) only eighth and posterior part of seventh pair of pleural bones meet at midline of carapace; (f) anterior plastral lobe truncated; (g) triangular intergular scute not overlapping anterior end of entoplastron and only partially separating the gular scutes along the midline axis of the plastron (Wood, 1983). The occurrence of two pelomedusid specimens with a midline keel on the carapace indicates the presence of an as yet undetermined species of *Kenyemys*.

Family Trionychidae

Tribe Cyclanorbini

Cyclanorbis Grey, 1854

Cyclanorbis turkanensis Meylan et al., 1990

KANAPOI MATERIAL. 17196, carapace missing the eight pair of costals and the lateral portions of all the left costals (holotype).

Only one specimen (the holotype) of this taxon

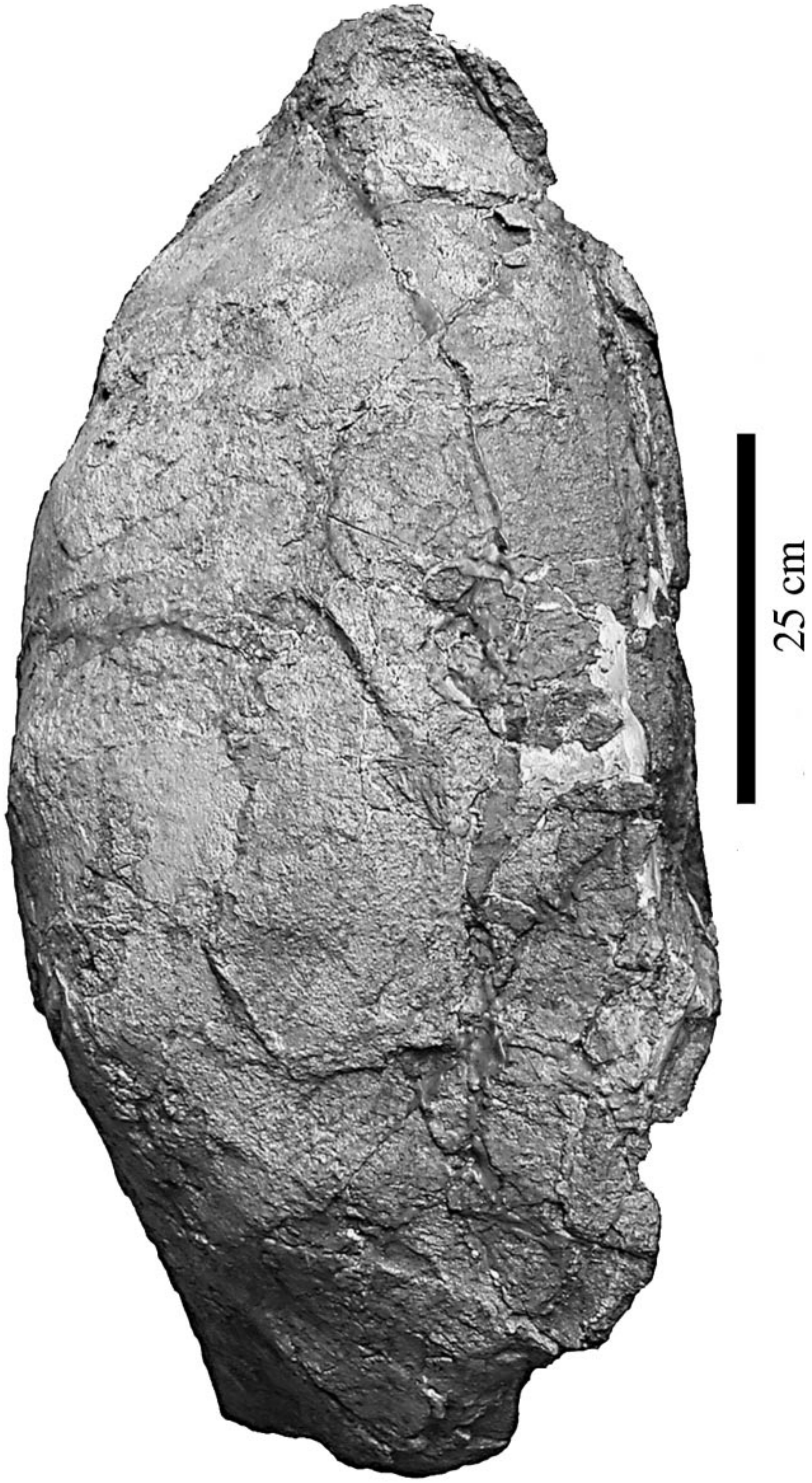

Figure 1 KNM-KP 10552; *Geochelone crassa* shell, dorsolateral view; scale = 25 cm

is known from Kanapoi. The distinctly concave lateral margins of the carapace posterior to the fourth costal together with the hypertrophied and distinctly V-shaped cross-section of the vertebrae centra distinguish this species from other species of *Cyclonorbis*.

Cyclanorbini gen. and sp. indet.

KANAPOI MATERIAL. 17202, carapace.

A relatively complete cyclanorbin carapace unfortunately lacks the diagnostic scutes that would permit identification beyond the tribal level.

Trionychidae gen. and sp. indet.

KANAPOI MATERIAL. 30605, carapace and plastron frags.

This specimen comprises fragments of carapace and plastron of a single individual that have the sculpted morphology characteristic of trionychid turtles but which cannot be identified beyond the family level.

Family Testudinidae

Geochelone Fitzinger, 1835

Geochelone crassa Andrews, 1914

(Figure 1)

KANAPOI MATERIAL. 10552, complete shell; 30199, carapace and plastron.

Geochelone is an almost cosmopolitan tortoise genus in which the carapace and plastron are never hinged and which often achieved large size. *Geochelone crassa* is a large (>700 mm PL) African form in which the pectorals are widest at the midline but narrow considerably on either side of the midline; gulars and pectorals fall short of the entoplastron. This species is based on a partial plastron from the early Miocene locality of Karungu (Meylan and Auffenberg, 1986:281) but evidently survived into the Pliocene. Meylan and Auffenberg (1986) identified KP 10552—a nearly complete but crushed, meter-long shell of a large land tortoise—as *G. crassa* (Fig. 1) but erroneously documented the accession number as 10052. They noted that most of the shell was badly broken but sulci and bone sutures are visible on the ventral surface of the anterior lobe of the plastron. The pectorals are widest at the midline (110 mm) but narrow laterally (to 30 mm). The gular scutes appear to reach the entoplastron but the pectorals do not.

cf. *Geochelone* sp. indet.

KANAPOI MATERIAL. 30439, carapace and plastron; 30614, half carapace and plastron.

Several specimens comparable in size to, or smaller than, the extant leopard tortoise *Geochelone pardalis* Bell, 1828 were recovered from Kanapoi by National Museums of Kenya expeditions.

Order Crocodylia

Family Crocodylidae

Crocodylus Laurenti, 1768

Crocodylus niloticus Laurenti, 1768

(Figure 2)

KANAPOI MATERIAL. 18333, Lt. mand frag; 18334, Lt. mand frag; 18336, incomplete skull; 18337, young skull; 18338, adult skull; 30196, articulated skull and mand; 30437, skull frags; 30492, cranial frags, scutes, and p/c frags; 30594, partial skull and mandible; 30604, skull.

The extant Nile crocodile is a moderate- to large-sized crocodylid with generalized rostrum of moderate proportion, median nasal promontorium, typically 14 maxillary and 15 mandibular teeth and with the anterior nuchal osteoderms well developed (Storrs, 2003). Ten relatively complete *Crocodylus niloticus* crania and/or mandibles were collected by National Museums of Kenya expeditions (Fig. 2). Tchernov (1976, 1986) had reported that the broad-snouted *Rimasuchus lloydi* (Fourteau, 1920) was the common crocodilian in the Lake Turkana Basin and that *C. niloticus* had a very sparse record in the Plio–Pleistocene. However, Storrs (2003) documented the presence of five crocodilian taxa, including both *R. lloydi* and *C. niloticus* at Lothagam. Even so, it was somewhat surprising to find ten *C. niloticus* cranial specimens in the Kanapoi biota but only one of *R. lloydi.* Nevertheless, the apparent dominance of the extant Nile crocodile in the Kanapoi biota must be viewed with caution because only the more complete crocodilian specimens were collected.

?*Crocodylus* sp. indet.

(Figure 3)

KANAPOI MATERIAL. 30451, rostrum and symphysis frags.

Associated rostrum and symphysis fragments document the presence of a second species of broad-nosed crocodile. This species can be distinguished from broad-nosed crocodilians previously documented from the Pliocene of East Africa by its unusually long mandibular symphysis. *R. lloydi* and the extant species *C. niloticus* and *C. cataphractus* Cuvier, 1824, all have short mandibular symphyses whereas that of KP 30451 is more than 10 cm long. This undetermined species is also characterized by the broad and straight anterior margin of the snout. No other fossil or extant crocodilian species is known to possess this combination of features (G. Storrs, personal communication).

Rimasuchus Storrs, 2003

Rimasuchus lloydi (Fourteau, 1920)

(Figure 4)

KANAPOI MATERIAL. 30619, anterior rostrum and mandible frags.

Figure 2 KNM-KP 18338; *Crocodylus niloticus* cranium, dorsal view; scale = 5 cm

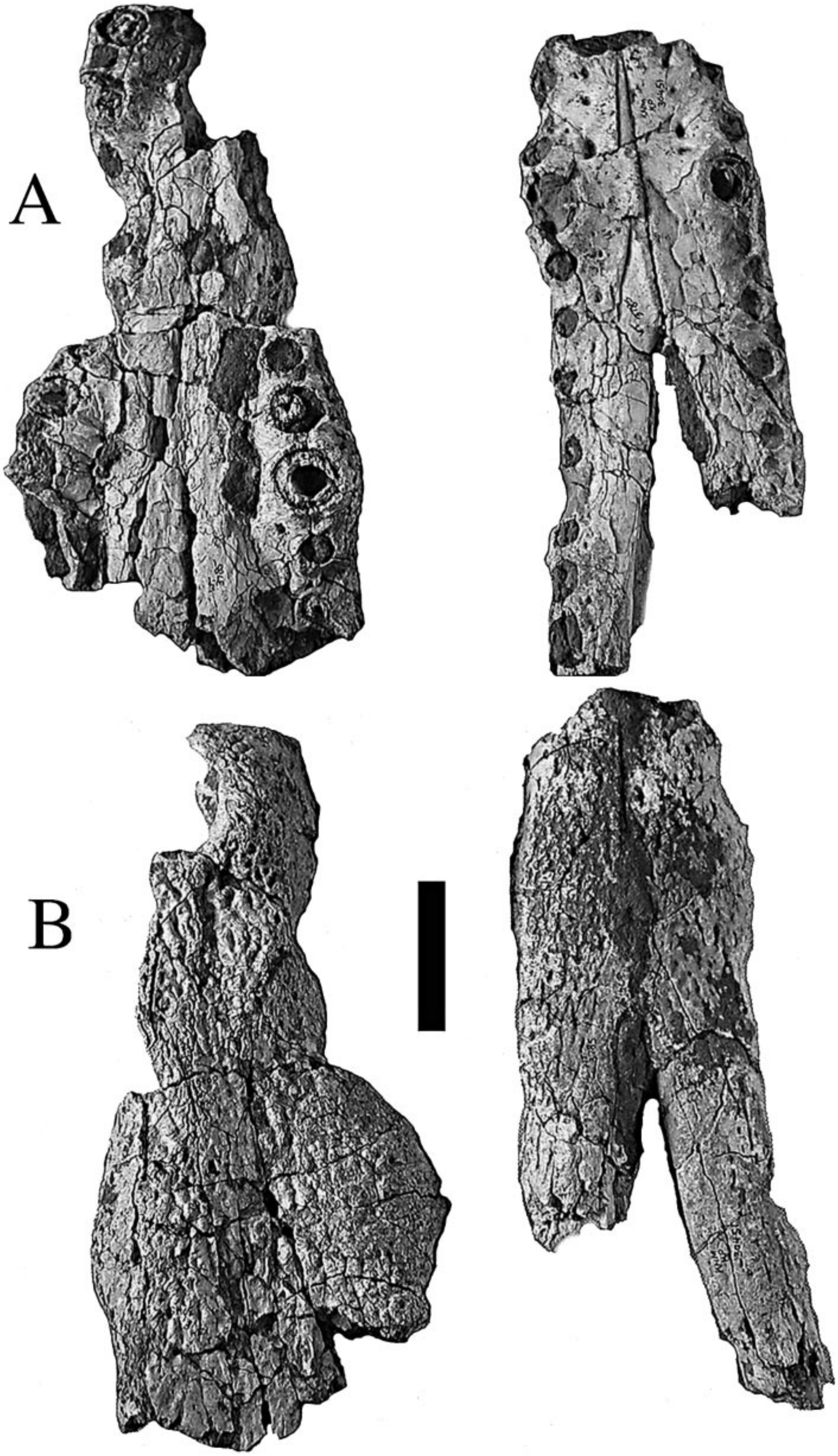

Figure 3 KNM-KP 30451; ?*Crocodylus* sp., cranium and mandible fragments; **A** = occlusal views of anterior rostrum and mandibular symphysis; **B** = dorsal view of anterior rostrum, ventral view of mandibular symphysis; scale = 5 cm

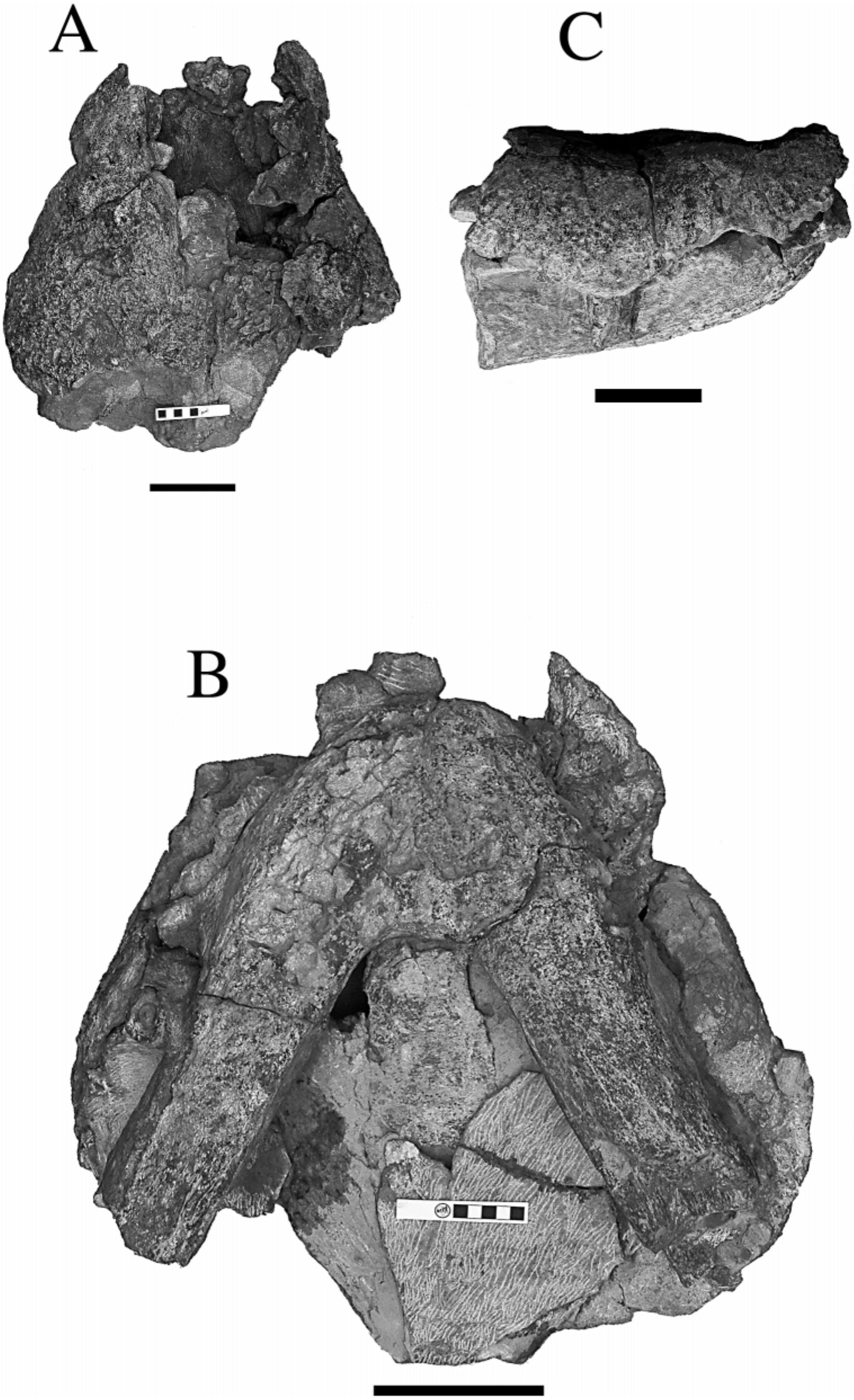

Figure 4 KNM-KP 30619; *Rimasuchus lloydi*, anterior rostrum and mandible fragments, **A** = dorsal view; **B** = ventral view; **C** = lateral view; scales = 10 cm

The genus *Rimasuchus* was proposed by Storrs (2003) for a very large, brevirostrine crocodylid that had been previously referred to *C. lloydi*. The species is characterized by premaxillae that are broader than long and that had a relatively straight premaxillae/maxillae palatal suture, a deep "canine" occlusal notch, a slight dorsal maxillary boss, closely spaced anterior dentary teeth, broadly diverging mandibular rami, and prominent dentary festoons. It is readily distinguished from *C. niloticus* by the lack of a nasal promontorium.

An anterior portion of a very large rostrum with associated mandible was recovered from just below the Kanapoi Tuff. Measuring 326 mm across the widest preserved portion of the anterior rostrum, the specimen represents the largest crocodylian individual yet recovered from the Lake Turkana Basin. The most distinctive features of *R. lloydi,* other than the absence of a nasal promontorium, are its relatively short but broad premaxillae and its short and deep mandibular symphysis. The conformation of the Kanapoi specimen leaves no doubt that it represents *R. lloydi.*

Euthecodon Fourtau, 1920

Euthecodon brumpti (Joleaud, 1920)

KANAPOI MATERIAL. 18330, complete skull and mand; 18331, rostrum frag; 18332, articulated skull and mand frag; 30653, mand symphysis; 30176, edentulous mand; 30266, mand frags; 30407, mand.

Euthecodon brumpti is a very large eusuchian in which the extremely elongate and narrow rostrum has deeply scalloped dental margins. The premaxillae and nasals are attenuated but the narial ridge is prominent. A moderate premaxillary/maxillary diastema is located behind four premaxillary teeth. The skull table is small and nearly square, the occiput vertical, the mandibular symphysis long, and the teeth isodont and slender (Storrs, 2003).

Half a dozen specimens of slender-snouted crocodilians were recovered by National Museums of Kenya expeditions. These clearly belong to *E. brumpti,* a species distinguished by its slender snout and long slender curved teeth, rather than to the gavial reported by Storrs (2003) from the lower Nawata Formation at the nearby site of Lothagam.

Order Struthioniformes

Family Struthionidae

Struthio Linnaeus

Struthio sp. indet.

KANAPOI MATERIAL. 29300, eggshell frags; 30221, eggshell frags; 30223, eggshell frags; 30262, eggshell frags; 30490, eggshell frags; 32522, eggshell frags; 36599, eggshell frags.

Several occurrences of fossil ostrich eggshell fragments were noted on the surface of the fossiliferous strata at Kanapoi and several voucher specimens were collected by National Museums of Kenya expeditions. These shell fragments all had the struthious pore pattern characteristic of living ostriches (Sauer, 1972) and the pore basins are of similar size and shape to those reported from the upper Nawata at Lothagam (Harris and Leakey, 2003a). The $\delta^{13}C$ content of the fossil eggshell is more negative than those of extant ostriches from Kanapoi and the $\delta^{18}O$ is more positive. It would appear that there was a greater proportion of C_3 vegetation in the Pliocene ostrich diet compared with that of modern ostriches on the west side of Lake Turkana.

Order Pelecaniformes

Family Anhingidae

Anhinga Brisson, 1760

Anhinga sp. indet.

KANAPOI MATERIAL. 39325, Lt. humerus.

This family is represented by the left humerus of a darter of comparable size to the extant African darter.

Order Ciconiiformes

Family Ciconiidae

Mycteria Linnaeus

Mycteria sp. indet.

KANAPOI MATERIAL. 30231, Lt. dist tibia, prox Rt. tibiotarsus, Lt. radiale, and long bone frags.

Storks were represented at Kanapoi by a single association of long bone fragments.

Order Charadriiformes

Family Anatidae

Gen. and sp. indet.

KANAPOI MATERIAL. 39326, proximal Lt. humerus.

The Anatidae was represented at Kanapoi by a goose-sized left humerus fragment.

Order Primates

Family Galagidae

Galago Geoffroy, 1796

The modern species range in size from the largest *Galago crassicaudatus* Geoffroy, 1812 (1,122–1,750 g) to the smallest, *Galago demidovii* (Fisher, 1806) (69–81 g), and they inhabit a variety of habitats including primary and secondary lowland and montane forests, gallery forests, *Acacia* woodlands, savannahs, thorn scrub, and forest edge.

cf. *Galago* sp. indet.

(Figure 5)

KANAPOI MATERIAL. 30260 Rt. mand frag. (M_2).

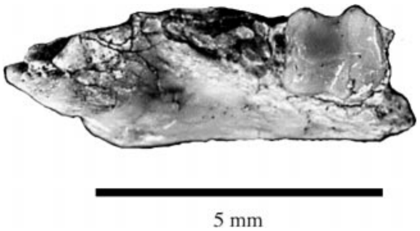

Figure 5 KNM-KP 30260; cf. *Galago* sp. indet., right mandible fragment (M_2), occlusal view; scale = 5 mm

Mandibular fragment, KP 30260, is approximately the size of *Galago demidovii,* the smallest living galago. The specimen is too fragmentary to allow precise identification. Due to their small size, galagos are rare in the fossil record and little is known of their distribution or evolution in the Pliocene.

Family Cercopithecidae

Subfamily Colobinae

Although rare elements in fossil assemblages, the Colobinae were a diverse group in the Pliocene, at which time they appear to have undergone a major radiation. Several species of large colobines are known from Pliocene and early Pleistocene deposits in the Turkana Basin, the Baringo Basin, and from Olduvai (Leakey, 1982, 1987). The postcranial morphology indicates differing degrees of arboreality but all appear to have been more terrestrial than extant east African colobines. Fossil Colobinae include at least three genera—*Paracolobus* Leakey, 1969, *Rhinocolobus* Leakey, 1982, and *Cercopithecoides* Mollet, 1947—and are known from several relatively complete skeletons. Smaller colobines were also diverse but are less well represented by fossils. The genus *Kuseracolobus* Frost, 2001 has been described from early Pliocene deposits at Aramis in the Awash Valley, Ethiopia, where colobines constitute an unusually high proportion (56%) of the cercopithecid assemblage. At Kanapoi, at least three species are represented, two moderately large but of indeterminate affinities, and the other an indeterminate species of *Cercopithecoides.* Such diversity at Kanapoi indicates that the colobine radiation began prior to 4.1 million years ago.

Cercopithecoides Mollet, 1947

Cercopithecoides is one of the best-represented colobine genera in the East African Pliocene and early Pleistocene. Until recently, only two East African species were recognized, *C. williamsi* Mollet, 1947, and *C. kimeui* Leakey M. G., 1982, but additional taxa are now described from Lothagam (Leakey et al., 2003) and at Leadu in Ethiopia (Frost and Delson, 2002). Features of the postcranial anatomy indicate that *Cercopithecoides* was probably the most terrestrial of the Pliocene colobines.

cf. *Cercopithecoides* sp. indet.

(Figure 6; Tables 1, 2, 4)

KANAPOI MATERIAL. 29255, mandible (Rt. P_3–M_3, Lt. P_3–M_1); 31741, broken M^1 or M^2; 32870, Lt. P_4; 36967, Lt. M^3; 37382, Rt. /C; 43120, P_3 talonid.

A handful of specimens represent a small species of colobine. The well-preserved mandible permits tentative taxonomic assignment to *Cercopithecoides.* The mandible probably represents a female: although the canines are lost, their alveoli are not large and the honing facet of the P_3 is short. The symphysis is broken toward the alveolar margin, the right body extends behind the M_3, and the left body terminates behind M_1. The M_1s are quite heavily worn, the M_2 and the premolars less so, and the M_3 has relatively light wear. Slight damage to the body beneath the P_3s on both sides may well be from carnivore chewing.

The mandibular morphology is similar to that of *Cercopithecoides* with a relatively shallow and moderately thick mandibular corpus. However, the anterior face of the symphysis lacks a median mental foramen and is more sloping and less flattened than in other known species. Below the deep genioglossal pit, the inferior torus is well developed. Although the canines are missing and the alveoli damaged, the dental arcade appears to be narrower between the canine alveoli. The inferior margin of the mandibular body is clearly defined anteriorly where there is a distinct and deep digastric fossa that merges posteriorly with the submandibular fossa. The mylohyoid line is prominent, providing considerable strength to the body and defining the upper extent of the submandibular fossa. With the exception of the less worn M_3, the teeth are heavily worn, as is so often the case with *Cercopithecoides.*

Colobinae gen. et sp. indet. A

(Figure 7; Tables 1–3)

KANAPOI MATERIAL. 31736, skull frag and male associated lower teeth (I, and Lt. P_4, partial Lt. and Rt. C, Rt. P_3, and molar, and molar frag); 29307, Rt. juv mand (dP_4, I_1–P_4 in crypts); 30408, Lt. mand (erupting P_3 and P_4, M_{1-2}); 30496, Lt. /C; 32803, Rt. $M_{1 \text{or} 2}$; 32525 male partial Lt. C/; 32821, Lt. M_2; 36830, Lt. mandible (M_1, crypt for M_2).

The specimens assigned to this taxon are fragmentary, largely subadult, and mostly from the lower jaw. They represent a fairly large colobine that has relatively large high-crowned premolars (compared with the size of the molars). The unerupted P_3 of KP 30408 has a large protoconid and distinct metaconid as well as a large distal fovea. The remaining specimens are tentatively referred to this taxon but could equally well belong to the following taxon.

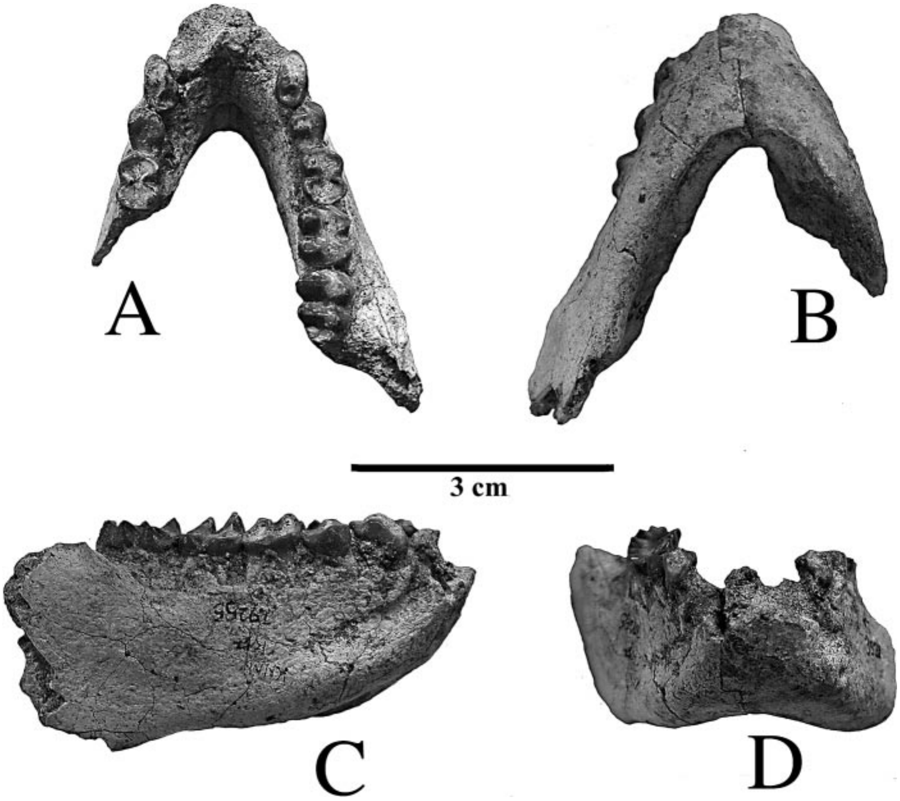

Figure 6 KNM-KP 29255; cf. *Cercopithecoides* sp. indet., mandible (Lt. P_3–M_1, Rt. P_3–M_3), **A** = occlusal view; **B** = inferior view; **C** = right lateral view; **D** = anterior view; scale = 3 cm

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Colobinae gen. et sp. indet. B

(Figure 8; Table 2)

KANAPOI MATERIAL. 29308, male Lt. mand (erupting P_3, roots C, P_4–M_1).

This is a juvenile mandible with the P_3 erupting. Although of similar size, the P_3 differs significantly from that of Colobinae gen. et sp. indet. A. It has a large single cusp, the protoconid, and a small distal fovea in contrast with the two cusps and large distal fovea of KP 30408.

Table 1 Kanapoi Colobinae upper dentition measurements

	M^3	
cf. *Cercopithecoides* sp. indet.	**MD**	**LL**
36967	8	8.2
	C/	
Colobinae gen. et sp. indet. A	**MD**	**LL**
32525	7.3	12.9

Subfamily Cercopithecinae

Tribe Papionini

The Papionini are the dominant cercopithecids in most Pliocene and Pleistocene sites in East Africa. *Parapapio* Jones, 1937, was the common genus in the early Pliocene, but was later replaced by *Theropithecus* Geoffroy, 1843. At Aramis, in the Middle Awash, a new 4.4 million year old papionin, *Pliopapio alemui* Frost, 2001, has been recovered (Frost, 2001). *Pliopapio* Frost, 2001, is distinguished from *Parapapio* by the presence of an anteorbital drop, a distinct ophryonic groove, and a shorter and more rounded symphysial profile. The absence of an anteorbital drop is the sole diagnostic character separating *Parapapio* from *Papio* Müller, 1773.

Genus *Parapapio* Jones, 1937

Parapapio is recorded from almost all East African Pliocene sites, and is generally believed to have given rise to *Papio,* from which it can be differentiated only by its facial profile. A number of species have been described and differ largely on the basis of size—a criterion that is not easy to apply when

Table 2 Kanapoi Colobinae lower dentition measurements

		I_1		/C			P_3			P_4		M_1		M_2		M_3	
	Side	**MD**	**LL**	**MD**	**LL**	**Max height**	**MD**	**BL**	**Height**	**MD**	**BL**	**MD**	**BL**	**MD**	**BL**	**MD**	**LL**
cf. *Cercopithecoides* sp. indet																	
29255	L						5.8	4.3		5.9	5	7.1	5.8				
29255	R						<6.5	4		6	4.8	7.1	5.9	8.7	6.7	10.2	6.4
31741														7.9			
32870										6.3	4.7						
37382 Female	R			6.6	3.4												
43120 Male	R							5.8									
Colobinae gen. et sp. indet. A																	
30408							9.1	6	11	>7.0	>6.0	9.5	6.7				
30496	L			10.7	7.9	16.4											
31736		4	5.7	10.4e	5.1	16.6				6.3	5.1						
32803	R													9.6	7.5		
32821	L													9.8	7.6		
36830	L											8.5	6.1				
Colobinae gen. et sp. indet. B																	
29308							6.8	4.6	>12.3								

Table 3 Kanapoi Colobinae gen. et sp. indet. A deciduous teeth

	dP_4	
Lower dentition	**MD**	**BL**
29307	6.6	4.7

there is some degree of sexual dimorphism. *Parapapio* was the most common cercopithecid in the South African Pliocene and early Pleistocene sites where *P. jonesi* Broom, 1940, *P. broomi* Jones, 1937, and *P. whitei* Broom, 1940, are recognized. In East Africa, *Parapapio* is less well known but, prior to the appearance of *Theropithecus,* is the dominant cercopithecid at most Pliocene sites in the Turkana Basin (e.g., Allia Bay, Kanapoi, and Lomekwi). *Parapapio ado* (Hopwood, 1936) is recognized at Laetoli, Tanzania (Leakey and Delson, 1987) and *Parapapio* cf. *P. jonesi* at Hadar (Frost and Delson, 2002).

Parapapio ado (Hopwood, 1936)

(Figure 9; Tables 5–8)

KANAPOI MATERIAL. 286, male mandibular symphysis (roots Lt. and Rt. I_1–/C), Lt. mandibular frags (P_4–M_1), (M_3), Rt. mandibular frag ($M_{2–3}$); 26942, Rt. mand ($M_{1–3}$); 29295, Rt. M_2; 29304, Lt. mand frag (worn $M_{1–2}$, M_3 talonid); 29305, Rt. M_3; 29306, male Lt. mand (P_3–M_3, root /C, alveoli Lt. and Rt. I_1–I_2); 29310, Rt. M^2; 29312, Lt. mand frag ($M_{2–3}$), Lt. P_4, mand and tooth frags; 30147, male edentulous mandibular symphysis (roots Lt. and Rt. C, P_3, alveoli Lt. and Rt. $I_{1–2}$), frags Lt. mandible (roots $M_{1–3}$); 30148, Rt. female C/; 30149, juvenile mand (Lt. d/C, $dP_{3–4}$, M_1, Rt. dI_2–M_1), Lt. juvenile max (dC/, $dP^{3–4}$, M^1, C/ in crypt), Rt. juvenile max (dP^3–M^1) isolated Lt. and Rt. dI^1, I^1, Rt. dC/, skull frags; 30213, Rt. M_2; 30230, female Rt. mand (P_3–M_3), Lt. mand ($M_{1–3}$), isolated Lt. and Rt. I_1, I_2 and Lt. P_3; 30233, Lt. male mand (M_3, roots /C–M_2), Rt. mand frag (root /C); 30398, worn and broken Rt. M_2 and mand frag; 30399, Rt. M_3; 30434, Rt. dI^1; 30483, Lt. M_3; 30531, squashed anterior female mand (broken Lt. and Rt. I_1–P_4); 30532, Lt. mandible (broken P_4–M_2); 30535, Rt. M_3; 29311, Lt. I^2; 30538, female max, mand, and skull frags: Rt. mandible (broken and

Table 4 cf. ***Cercopithecoides*** **sp. indet mandibular measurements**

	29255
Depth below P_4/M_1 junction	20.9
Depth below M_2/M_3 junction3	21.4
Max thickness below M_1	10.4
Max thickness below M_3	10.9
Length tooth row P_3–M_3	39.8

Figure 7 KNM-KP 30408; Colobinae gen. et sp. indet. A, left mandible, occlusal view; scale = 2 cm

Figure 8 KNM-KP 293080; Colobinae gen. et sp. indet. B, left mandible, occlusal view; scale = 2 cm

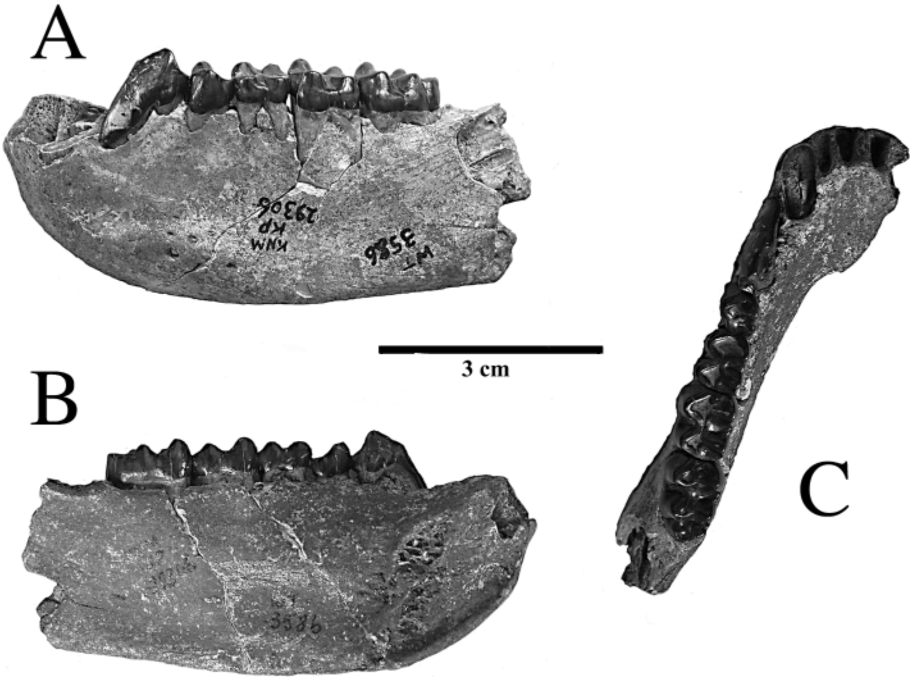

Figure 9 KNM-KP 29306; *Parapapio ado*, left male mandible (P_3–M_3), **A** = lateral view; **B** = medial view; **C** = occlusal view; scale = 3 cm

cracked I_1–M_3), Lt. mandible (I_2–M_1), Lt. I_1, M_3, /M; Lt. maxilla (I^1–P^3) broken Rt. C/, broken Lt. P^4, M^1, M^2, M^3; 30539, Rt. M_1; 32512, Lt. M^3; 32520, female edentulous mand (roots Lt. I_1–M_1 and Rt. I_1), Rt. I_2; 32527, Lt. dP^4; 32534, Rt. M^1 or M^2; 32535, Rt. M_2; 32554, Rt. male C/; 32572, Lt. dP_4; 32804, mesial frag Lt. M_3; 32805, partial Rt. M^1; 32806, Rt. M_3; 32811, broken Rt. M_3; 32816, Rt. I_1; 32817, worn Rt. M_3; 32819, Rt. max (P^{3-4}), frag edentulous Lt. premax; 32869, Rt. M_3, and Lt. /C; 32878, Rt. dP^3; 32884, Lt. d/C; 36914, Lt. M_2, partial /M; 36969, Rt. female /C, M frag, Lt. P^4; 37374, tooth frags—molar and premolar upper and lower, dist phalanx; 37378, broken M, tooth frag; 37379, Lt. /I, talonid Lt. M_3; 37380, broken Lt. I_2; 43121, Rt. female /C; 43122 dP_4.

The Kanapoi *Parapapio* material is rather fragmentary and consists mainly of isolated teeth. Two mandibular specimens are well preserved in addition to the mandible KP 286 that was recovered by the earlier expeditions and initially attributed to *Parapapio jonesi* (Patterson, 1968). KP 29306, a male left mandibular body, includes the entire symphysis extending to the right canine alveolus. The symphysial morphology is close to that of KP 286, although it is shallower and in profile less steeply inclined with a slight curvature. The body is not deep and is quite slender with well-preserved P_3–M_3. KP 30147 is a mandibular symphysis that has suffered some postmortem expansion, making it appear larger than KP 286. If allowance is made for the distortion, the symphysial morphology is similar to the other two specimens. All three mandibles have a distinct mental foramen and may be distinguished from *Pliopapio alemui* by the steeply sloping symphysis and the angle of the incisor roots, which shows the incisors to have been procumbent rather than vertically set. Two specimens, KP 30149 and KP 30538, have well-preserved upper and lower juvenile dentitions.

The M_3 has an unusually large talonid and talonid basin, such that the hypoconulid is of almost equal size or in some cases (KP 30233) larger than the distal lingual cusp (entoconid). This feature, which occurs with a relatively high frequency at Kanapoi but is unusual in other species of *Parapapio,* may possibly be of taxonomic significance.

Theropithecus Geoffroy, 1843

Theropithecus first appears in the Turkana Basin about 3.5 million years ago, although one older tooth from Allia Bay may possibly represent this genus and a partial tooth from Kanapoi is here assigned to *Theropithecus*. At Pliocene localities younger than 3.5 million years, *T. brumpti* (Arambourg, 1947) became the dominant cercopithecoid until it was replaced by *T. oswaldi* (Andrews, 1916) at about 2.5 million years (Leakey, 1993).

cf. *Theropithecus* sp. indet.

KANAPOI MATERIAL. 32879, broken Rt. $M_{1\text{ or }2}$.

Table 5 Kanapoi *Parapapio ado* upper teeth measurements

			I¹		I²		C/			P³		P⁴		M¹		M²		M³	
		Side	MD	LL	MD	LL	MD	LL	Height	MD	BL	MD	LL	MD	BL	MD	BL	MD	LL
29310																		9.6	9.3
29311					4.2	5.3													
30148	Female	R					6.8	6.8	10.9										
30149		L	7.5	6.0	~4.8	4.4								9.3	8.1				
30149		R	7.5	~5.8										9.3	8.0				
30538	Female	L	6.5	6.1	>3.9	4.9	>6.3			6.7	5.0	5.7	7.0	8.2		9.8		9.5	9.5
30538		R					>5.9	5.6											
32512		L																10.6	10.1
32534																>10	8.6		
32805																8.3	>6.8		
32819		R								>5.3	7.1	5.3	7.4						
32554		R					11.6	8.8											
36969		L										5.6	7.4						

This tooth is larger than any of the *Parapapio* first and second molars (MD length 11.6; BL distal breadth 8.0). It is incomplete, lacking most of the lateromesial cusp both mesial and lateral to the preserved cusp tip. The deep valleys and high cusps indicate affinities with *Theropithecus*. As such, this is one of the earliest occurrences of this genus.

Cercopithecidae gen. et sp. indet.

(Figure 10)

KANAPOI MATERIAL. 458, prox Lt. ulna, dist femur; 29292, partial Lt. femur shaft; 29303, dist Rt. humerus; 29309, Lt. astragalus; 30424, prox Rt. femur; 30431, prox Rt. radius; 30460, prox Lt. femur; 30529, prox Rt. femur; 32516, Lt. C/; 32562, phalanges, phalanx shaft, prox m/p, patella, rib frags; 32818, frags of calcaneum, femur head, long bone frags; 32880, caudal vertebra; 36601, proximal phalanx; 36831, prox Lt. ulna frag; 36834, distal Rt. humerus; 36837, Rt. astragalus.

A complete, slender, high-crowned canine (KP 32516) represents a small monkey. Crown measurements are MD length, 3.9; LL width, 6.3; max crown height, 13.0. The height of the crown suggests it must be from a male. The size is too small for it to belong to the Kanapoi *Parapapio*. It may possibly be referable to cf. *Cercopithecoides* sp. indet., the small colobine described above, but the slender nature of the canine is unlike other colobines. For now it is left as Cercopithecidea gen. et sp. indet.

Two fragments of distal humerus are morphologically similar but very different in size. The mediolateral width of the smaller, KP 29303, is 22.5 mm, in contrast with the larger KP 36834, which measures 30.4 mm. Both are reasonably well preserved although, on both, there is some weathering of the medial epicondyle and along the lateral edge of the capitulum. The trochlear flange is relatively lightly developed and the olecranon fossa elongated lateromedially, quite deep but not perforated. Compared with the *Parapapio lothagamensis* humeri described from Lothagam (Leakey et al., 2003), the medial epicondyle is less posteriorly directed, the trochlear flange less strongly developed, and the olecranon fossa more elongated lateromedially without any proximal extension to accommodate the ulna olecranon process in extension. The distal humerus of *Cercopithecoides* is closer in all these characters to those from Lothagam than to the two specimens from Kanapoi.

Two partial ulnae were recovered, KP 458 and KP 36831. The former is well preserved, small, lightly built, and most probably colobine. Its short olecranon process is slightly deflected posteromedially. The radial notch appears to show some indication of a double articular facet. KP 36831 is slightly larger, less well preserved, and squashed, but is morphologically similar to KP 458.

The shaft of the proximal radius, KP 30431, extends 30 mm below the radial tuberosity. The ar-

Table 6 *Parapapio ado* lower dentition measurements

			I_1		I_2		/C			P_3			P_4		M_1		M_2		M_3	
		Side	MD	LL	MD	LL	MD	LL	Max height	MD	BL	Height	MD	BL	MD	BL	MD	BL	MD	LL
00286	Male	L				~5.8	10.0						>5.8	6.1	7.8	7.3			12.5	9.7
00286	Male	R															10.8	8.4	12.2	9.1
06942		R													8.4	7.2	11.3	9.1	13.8	9.0
09295		R															9.5	8.1		
09304		L													6.6	6.4	8.7	8.0		
29305		R																	10.9	7.3
29306	Male	L								7.8	4.9	15.3	6.7	5.5	8.1	6.6	10.0	8.2	11.5	8.8
29312		L															11.4	9.4	12.1	9.0
30149		L													8.1	~6.8				
		R													8.3					
30213		R															10.4	8.1		
30230	Female	L	4.2	5.2	3.6	5.2				>6.1	4.3					10.4	8.3	11.8	8	
	Female	R	4.1	5.3	3.9	5.4				6.5	4.3	4.3	6.9	7.6		10.2	8.3	>11.7		7.9
30233		L																	12.9	8.8
30398		R															10.5	<8.7		
30399		R																	13.3	8.7
30483		L																	13.0	9.1
30531	Female	L											6.5							
30532		L													7.6	>6.4				
30535		R																	13.2	9.0
30538	Female	L	4.3	5.3	3.5	5.4	3.5	6.2		5.3	>3.9		6.5	>5.5		9.5		11.7	8.5	
	Female	R	4.4	5.6	3.4	5.6							6.1	5.3	7.2				11.9	
30539		R													8.8	6.5				
32520	Female	R			3.6	4.6e														
32535		R															9.1	8.0		
32804		L																		8.7
32806		R																	10.9	7.4
32811		R																	12.3	
32816		R	4.3	4.8																
32817		R																	10.9	7.8
32869	Male	L					6.4	8.8	>14.1											
32869	Male	R																	12.1	>8.5
36914		L															9.9	8.4		
36969		R					3.9	7.7												
37379		R	4.0	5.5																
37380		L			>4.2															
43122		R								6.4	3.2									

Table 7 *Parapapio ado* deciduous teeth

		dI^1		dI^2		dC/			dP^3		dP^4	
	Side	MD	LL	MD	LL	MD	LL	Height	MD	BL	MD	BL
Upper dentition												
30149	L	6.0	3.6			5.2	3.7		7.5	6.0	8.5	6.9
30149	R	6.1	3.4			5.2	3.6		6.8	6	8.5	6.9
30434	R	5.8	3.6									
32572	L										7.3	6
32878	R								7	6.3		

		dI_1		dI_2		d/C			dP_3		dP_4	
	Side	MD	LL	MD	LL	MD	LL	Height	MD	BL	MD	BL
Lower dentition												
30149	L			4	2.8	3.5	4.2	>5.2	6.8	4.5	7.1	5.9
30149	R					3.6	4.3		6.9	4.4	7	6
32527	L										6.8	5.5
32884	L					2.9	4.3					
43122											6.5	5.2

ticular surface of the head is almost circular, with a distinct depression for articulation with the humerus capitulum. It is tilted with the posteriomedial edge higher than the opposite side; the anterolateral portion of the collar surrounding this depression is widest. The head measures 15.5 mediolaterally by 14.5 anteroposteriorly. The radial tuberosity is well developed with a raised and rounded anterior border and a less prominent crest marking the posterior margin. The interosseous crest commences about 10 mm below the most distal extent of the radial tuberosity.

Three fragments of proximal femora, KP 30460, 30424, and 30529, and a proximal femur shaft, KP 29292, have been recovered. 30460 has lost the margins of the greater tuberosity, 30424 lacks the head, and 30529 has lost both the greater and lesser tuberosities. KP 458 is a distal epiphysis with approximately 25 mm of shaft. The neck of KP 30424 is relatively long compared with those of the Lothagam femora, and the articular surface of the slightly larger head projects onto the femoral neck. The greater tuberosity of KP 30460 is relatively large and would have extended proximal to the head. KP 30529 is significantly smaller than the other fragments. The proximal shaft KP 29292 has a pronounced crest on the posterior face proximal to the commencement of the linea aspera.

Table 8 Kanapoi *Parapapio ado* mandibular measurements

	29306
Depth below P_4/M_1 junction	27.1
Depth below M_2/M_3 junction	24.7
Max thickness below M_1	9
Max thickness below M_3	9.3
Length tooth row P_3–M_3	35.4

Two complete tali were recovered. The maximum length of the smaller, KP 29309, is 23 mm; that of the larger, KP 36837, is 27 mm. KP 29309 has a carnivore tooth mark on its trochlear surface. Both specimens have relatively long necks.

The affinities of the postcranial elements are unclear. In general, they appear to be from similar sized individuals, but the size discrepancy between the two morphologically similar distal humeri suggests these elements may represent one sexually dimorphic species.

DISCUSSION

Sites close in age to Kanapoi that have yielded early cercopithecids include Aramis (4.4 Ma), Allia Bay (3.9 Ma), Laetoli (3.6 Ma), and the Sidi Hakoma (3.4–3.22 Ma), Denen Dora (3.22–3.18 Ma), and lower Kada Hadar (3.18–2.92 Ma) members of the Hadar Formation in the Awash Valley. Aramis is unusual in having a larger proportion of colobines to cercopithecines (56% colobines). Only two cercopithecoid species are recognized from Aramis—*Kuseracolobus aramisi* Frost, 2001, and *Pliopapio alemui*. Neither is represented at Kanapoi. The Allia Bay cercopithecids are largely represented by isolated teeth that are difficult to assign taxonomically. However, papionins far outnumber colobines. At Laetoli, the common cercopithecid is *Parapapio ado,* although cf. *Paracolobus* sp. is also relatively common. Unfortunately there are no well preserved P_3s in the Laetoli assemblage that can be compared with the two differing large colobine P_3s from Kanapoi. It is possible that one of the Kanapoi colobines is the Laetoli species. Present but uncommon at Laetoli was a small indeterminate co-

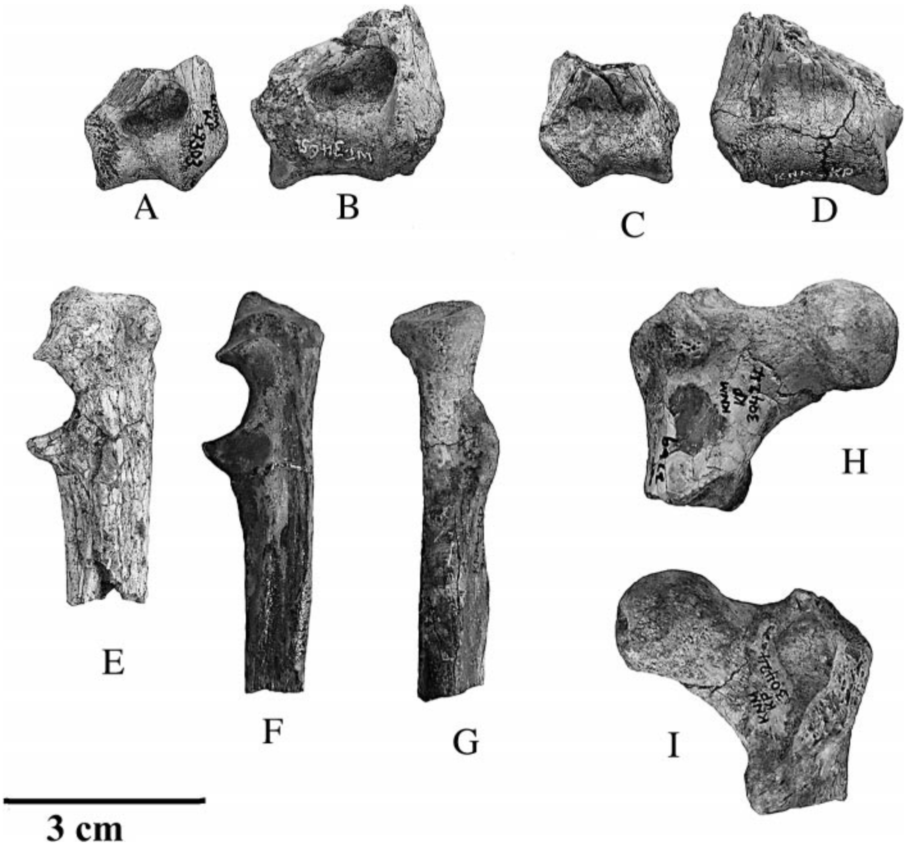

Figure 10 Cercopithecidae gen. et sp. indet., postcranial elements; distal right humerus: **A,C** = KNM-KP 29303, **B, D** = KNM-KP 36834; **A, B** = posterior view, **C, D** = anterior view; **E** = KNM-KP 458, proximal left ulna, **F** = KNM-KP 36831, proximal left ulna; **G** = KNM-KP 30431, proximal right radius, **E, F, G** = lateral view;. **H, I** = KNM-KP 30424, proximal right femur, **H** = anterior view, **I** = posterior view

lobine and a large papionin cf. *Papio* sp. (Leakey and Delson, 1987). The cercopithecids from Hadar include *Theropithecus darti* (Broom and Jenson, 1946) and *Parapapio* cf. *P. jonesi,* as well as the colobines *Rhinocolobus turkanaensis* Leakey M. G., 1982, and a new species of *Cercopithecoides* (Frost and Delson, 2002).

Table 9 Kanapoi *Deinotherium bozasi* tooth measurements

Accession No.		401	30152
Lt. M^2	ap	92.1	
	prot	92.4	
	met	90.8	
Lt M^3	ap	96.5	
	prot	99.0	
	met	90.1	
Lt. M$_3$	ap		87.5
	prot		79.9
	met		67.9

Family Hominidae

Australopithecus Dart, 1925

Australopithecus anamensis Leakey et al., 1995

KANAPOI MATERIAL. 271, distal Lt. humerus; 29281, holotype mandible and Lt. temporal; 29282, Lt. M$_{1/2}$; 29283, maxilla; 29284, Rt. P$_3$ and Rt. /C germs; 29285, Rt. tibia lacking midshaft region; 29286, mandible fragments and associated lower teeth (Rt. I$_1$, Lt. and Rt. I$_2$–M$_3$); 29287, mandible with teeth; 30498, Lt. and Rt. maxilla fragments and associated dentition; 30500, mandibular fragments and associated dentition (Rt. I$_2$–P$_4$, M$_{2–3}$); 30502, Rt. M$_3$, partial Lt. /M, molar frags; 30503, proximal manual middle phalanx; 30505, broken molar germ; 30942, five molar frags; 31712, associated juvenile mandibular and dental fragments; 31713, Rt. mandible with tooth fragments; 31714, Lt. dP$_4$; 31715, Lt. M$_{1/2}$ and two associated tooth frags; 31716, P$^{3/4}$ fragment and C/ frags; 31717, Lt. M^3, Rt. M$_3$, and Lt. M$_2$ frags; 31718, Rt. mandible frag (M$_{2-3}$); 31719, I^1; 31720, maxillary M fragment; 31721, Rt. M^2 and M^3 partial crowns; 31723, Rt. M^3; 31724, Lt. capitate; 31726, Rt. P^4; 31727, Rt. /C; 31728, Lt. M$_1$; 31729, Rt. dP$_2$; 31730, Lt. M$_2$, Rt. P$_3$; 31732, tooth frags; 34725, associated juvenile dentition and skull frags; 35838, Lt. M$_3$; 35839, Lt. I^1, Rt. C/, and Lt. P^3; 35840, Lt. M^3 and upper tooth frags; 35841, M crown; 35842, Rt. M$^{?1 \text{ or } ?2}$; 35844, M frag; 35845, M frag; 35847, Lt. M$_2$; 35850, M/ frag; 35851, Lt. M$^{1/2}$ frag; 35852, Lt. C/; 37522, Lt. /M; 37523, M frag; 37524, tooth frags.

Australopithecus anamensis is distinguished from all other australopithecine species by the following features: a small external acoustic meatus presenting a narrow ellipse in outline; long axes of mandibular bodies and tooth rows nearly parallel and close together; mental region of mandible not strongly convex; long axis of symphysis slopes markedly posterioinferiorly; canines with very long robust roots, trigons of upper molars much wider than talons, distal humerus with thick cortex enclosing a small medullary cavity. It can be distinguished from *A. afarensis* Johanson et al., 1978, by the following: upper canine root and associated facial skeleton less posteriorly inclined; lower molars tend to have more sloping buccal sides and upper molars more sloping lingual sides; tympanic plate horizontal without defining grooves. It can be distinguished from *Ardipithecus* White et al., 1994, by the following features: absolutely and relatively thicker enamel; upper canine buccal enamel thickened apically; molars more buccolingually expanded; first and second molars not markedly different in size; tympanic tube extends only to the medial end of the postglenoid process, rather than to the lateral edge or beyond it; lateral trochlear ridge of humerus weak (Leakey et al., 1995).

Australopithecus anamensis is the oldest reliably dated *Australopithecus* species. It was a habitual biped and is readily distinguishable from *A. afarensis* to which it may have been ancestral. A detailed account of the Kanapoi material, and of slightly younger material of *A. anamensis* from Allia Bay, was provided by Ward et al. (2001).

Order Proboscidea

Family Deinotheriidae

Deinotheres are Neogene proboscideans that differed from gomphotheriids and elephantids by retaining only the lower tusk and by never developing horizontal tooth replacement for their low-crowned lophodont teeth. Adapted for browsing on forest vegetation, they were common elements of the early Miocene African assemblages but are encountered only in small numbers in Pliocene and Pleistocene assemblages.

Deinotherium Kaup, 1829

Deinotherium bozasi Arambourg, 1934

(Table 9)

KANAPOI MATERIAL. 388, enamel frags and postcranial elements; 393, atlas; 401, Lt. M^2 and M^3; 30152, Lt. M$_3$; 30557, partial M.

Deinotherium bozasi was a large African deinothere with teeth of similar size to the European species *Deinotherium giganteum* Kaup, 1829. The skull rostrum was steeply downturned anteriorly (like that of *Prodeinotherium hobleyi* [Andrews, 1911]) but the external nares and rostral trough were narrower than in *D. giganteum.* As in *P. hobleyi* but in contrast with *D. giganteum,* the preorbital swelling is reduced and situated just in front of P^3, the occiput is steeply inclined, and the nasal bones have a slight anterior median projection (Harris, 1978).

Deinotheres are represented at Kanapoi by a couple of isolated teeth and, perhaps, by ribs and vertebrae of a juvenile proboscidean that were associated with unerupted deinothere enamel fragments. The upper second and third molars are distinctly smaller than the equivalent teeth on the somewhat younger *D. bozasi* skull from Koobi Fora (Harris, 1976a) and the lower third molar is smaller than the equivalent tooth in early Pleistocene deinotheres.

Family Gomphotheriidae

Gomphotheriids were the common proboscideans in African Miocene assemblages but only *Anancus* lingered into the early Pliocene.

Anancus Aymard *in* Dhorlac, 1855

Anancus kenyensis (MacInnes, 1942)

(Table 10)

KANAPOI MATERIAL. 384, Lt. M$_2$; 410, Lt. M$_2$, Lt. and Rt. M$_3$.

Anancus kenyensis has been diagnosed by Coppens et al. (1978) as "a progressive species of *Anancus* with four and one half to five or more cone pairs on M2 and five and one half or more on M3; the crown is complicated by the presence of enamel columns partially fused into the faces of the main cones."

Anancus kenyensis is the last gomphotheriid species to survive in sub-Saharan Africa. Three *Anancus* teeth were recovered from Kanapoi by the Patterson expeditions of 1965 and 1966. Tassy (2003) recognized two different populations of *A. kenyensis*—a primitive or *kenyensis* morph with tetralophodont second molars based on the holotype of *A. kenyensis*, from Kanam (MacInnes, 1942) and a derived or *A. k. petrocchi* morph with pentalophodont second molars based on the sample from Sahabi (Libya) described by Petrocchi (1954). The *A. kenyensis* morph was recognized in samples collected from Kanam, Lukeino, Mpesida, and

Table 10 Kanapoi *Anancus kenyensis* tooth measurements

Accession No.	384	410	410	410
Tooth	LM_2	LM_2	RM_3	LM_3
No. plates	5	5	6	
No. plates in wear	5	5	3	
Length	156.25	146.6	220	
Length wear surface			91.6	
Width (greatest)	75.89	68.64	81	79
Height (middle plate)	67.54		60.9	64.09
Enamel thickness			5.04	

Lothagam, whereas the *A. k. petrocchi* morph is represented at Sahabi (Libya) and at Aterir, and in the Chemeron Formation in the Baringo Basin, as well as at Lothagam. The second molars recovered from Kanapoi display the derived traits—accessory conules, fifth lophid, and strong anancoidy—that are characteristic of the *A. k. pettrochi* morph (Tassy, 2003).

Family Elephantidae

The Family Elephantidae originated in the late Miocene of Africa. *Stegotetrabelodon* Pettrochi, 1941, and *Primelephas* Maglio, 1970, are the dominant elephantids at Lothagam (Tassy, 2003). *Elephas ekorensis* Maglio, 1970, first appears in the Apak Member at Lothagam together with an early *Loxodonta* F. Cuvier, 1925, species. *Elephas ekorensis*, and *Loxodonta adaurora* appear to be the characteristic elephantids of the African early Pliocene.

Elephas Linnaeus

Elephas ekorensis Maglio, 1970

(Figure 11; Tables 11, 12)

KANAPOI MATERIAL. 382, Rt. P^4 frag; 392, P_2; 395, M_3 frag; 400, mand (P_2); 409, Rt. and Lt. mand frags (M_2); 411, Lt. M_3 frag; 412, M^2; 452, Rt. P^3; 28442, Lt. and Rt. P_3 frags; 30189, Lt. M^3; 30197, skull (RP^{2-3}, Lt. P^{2-3}); 30236, M^3; 30404, Rt. and Lt. P^{3-4}, skull frags; 30625, M_1 frag and unerupted M_2 frags; 30639, mand (Rt. M_2, Lt. M_{1-2}); 32575, Lt. mandible (P_{3-4}); 30198, Lt. mand (M_{1-2}); 387, RM_3; 26956, Rt. mand (M_1); 30169, Lt. juv mand (P_{2-3}); 30170, Lt. juv mand (P_3) and symphysis; 30173, Lt. mand frag (P_3), frags unerupted P_4; 30175, mand (Lt. P_3, dP_4, Rt. P_4); 30270, Lt. and Rt, P^{2-4} and tusk frag eaten by hyena; 30471, Lt. mand (M_2 and M_3) and symphysis; 38975, Rt M_3.

Elephas ekorensis is an early species of *Elephas* that was diagnosed by Maglio (1973) as having molars with crown height 10–15% greater than width, M3 broad anteriorly, becoming very narrow posteriorly; greatest width at base of crown; enamel loops prominent; enamel only very weakly folded near the base, 3–4 mm thick. The enamel plates are well separated with lamellar frequency of 3.8–4.8. The plate formulae are M3 11/12, M2 ?/?, M1 7/8 (Maglio, 1973).

Elephas ekorensis and *Loxodonta adaurora* are the two common proboscideans from Kanapoi. The teeth of *E. ekorensis* may be generally distinguished on the basis of their narrower width, greater number of plates, greater lamellar frequency, and thinner and more convoluted enamel (Fig. 11). Unworn tooth plates have more apical digitations than those of *Loxodonta* teeth. Mandibles of *E. ekorensis* are proportionately narrow; the ventral surface is horizontal but curves down in front of the symphysis to terminate in a beak, which curves abruptly anteroventrally and is smaller and more gracile than that of *L. adaurora*. The upper second premolar sometimes has two plates (KP 30197) but the lower has three (KP 30150). The third premolars have six plates and are wider posteriorly. The fourth premolar and first molar have eight plates.

Elephas ekorensis is one of the oldest recognized species of *Elephas*. It has been recovered from the Apak Member of the Nachukui Formation at Lothagam, where it is preceded in the Upper Nawata Member by *Elephas nawataensis* Tassy, 2003, which Tassy (2003) interprets as intermediate between the earlier *Primelephas gomphotheroides* Maglio, 1970, and *E. ekorensis*.

Loxodonta F. Cuvier, 1825

Loxodonta adaurora Maglio, 1970

(Figure 12; Tables 13, 14)

KANAPOI MATERIAL. 381, Lt. and Rt. mand (M_1); 383, Lt. and Rt. M^3; 383, Lt. M_3 and frags; 385, holotype mand and skeleton; 389, M^3 frags; 390, Rt. and Lt. M^3 frags; 391, M_1 frag and pc; 394, radius and ulna; 396, Rt M_2; 403, mand (Lt. M_{2-3}), pelvis, and femur; 406, Rt. mand frags (M_{1-2}); 407, RM_3; 548, Lt. M_3 frags; 28441, M^2 frag; 30150, P_2; $M_{2 \text{ or } 3}$ talonid; 30188, Rt. maxilla (worn M^3); 30191, max frag (Lt. M^3); 30193, Lt. and Rt. mand (M_3) and frags; 30204, skull (Rt. and Lt. M^3), damaged posteriorly; 30269, mand (Rt. and Lt. M_{2-3}); 30436, P_2; 30596, mand $M_{?3}$ (needs preparation); 30616, mandible (Lt. and Rt.

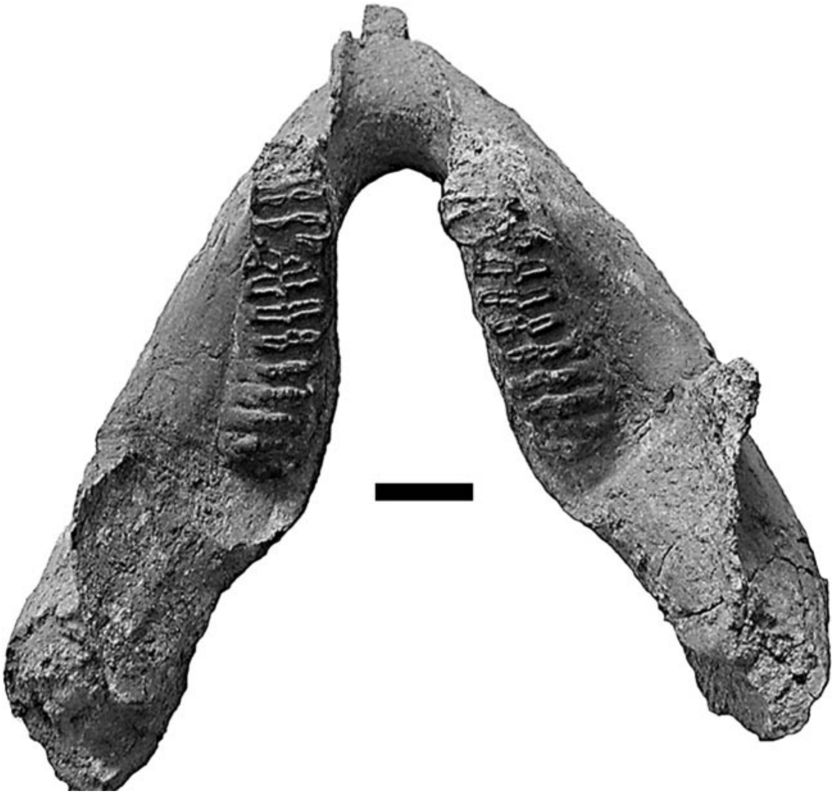

Figure 11 KNM-KP 30175; *Elephas ekorensis* mandible with Lt. P_3, P_4, Rt. P_4, occlusal view; scale = 5 cm

P_3, P_4); 30654, Rt. M_3; 32542, mand (Rt. and Lt. M_{2-3}).

Loxodonta adaurora was diagnosed by Maglio (1970) as a *Loxodonta* species with low-crowned molars, height equal to or less than width; enamel not folded, 3–5 mm in thickness; very large anterior and posterior columns, partially fused into plates but free at their apices, forming prominent median loops with wear; plates thick and well separated, lamellar frequency from 2.6 to 4.4. The plate formulae: M3 8–10X/10–11x, M2 7–8x/6–8x, M1 7/6–7 dm4 5/5–6, dm3 5/5–6, dm2 3/3 (Maglio 1973).

The holotype of *Loxodonta adaurora,* a skull and partial skeleton, was collected from Kanapoi in 1965 and described by Maglio in 1970 but unfortunately was badly damaged during its subsequent transportation back to Kenya. Some less complete specimens were collected by National Museums of Kenya expeditions during the 1990s. In general, *L. adaurora* teeth may be distinguished from those of *E. ekorensis* because they are wider, have fewer plates, and have thicker and less convoluted enamel; unworn tooth plates have a posterior median pillar and fewer apical digitations. The horizontal ramus of the mandible tends to be bulbous because of the greater width of the *L. adaurora* teeth. The ventral surface of the mandible curves downward anteriorly at the rear of the symphysis to terminate in a robust beak. The cusps of the second premolars tend to remain isolated rather than fused into transverse plates. Fourth premolars and first molars have seven plates.

Loxodonta exoptata (Dietrich, 1941)

(Figure 13)

Kanapoi Material. 30611, Rt. mandible (M_2).

Loxodonta exoptata was originally recognized from the 3.5 Ma Laetolil Beds of Laetoli in Tanzania (Beden 1987). The teeth are more hypsodont than those of *L. adaurora* and have more plates but thinner enamel. In early wear, the plates form a loxodont pattern strongly reminiscent of the extant *L. africana* (Blumenbach, 1797). Molar fragments attributed to *Loxodonta* aff. *L. exoptata* have been recovered from the Apak Member at Lothagam (Tassy, 2003).

A partial mandible with lower second molar from high in the succession is the sole representative of *Loxodonta exoptata* from Kanapoi. It has eight plates, each with a posterior median pillar,

Table 11 Kanapoi *Elephas ekorensis* upper teeth measurements

Accession No.		**30197**	**30197**	**382**	**30197**
Tooth		LP^2	RP^2	LP^3	LP^3
No. plates			5+		6
No. plates in wear			2		6
Length		24.75	23.57		68.7
Length wear surface			16.75		62.3
Width (widest plate)		23.12	21.29	40.24	
Height (middle plate)			37.74		
Enamel thickness			1.7		
Laminar frequency			9E		10

Accession No.	**30197**	**30404**	**30404**	**30404**	**30404**
Tooth	RP^3	LP^3	RP^3	LP^4	RP^4
No. plates	6	6	6	5+	5+
No. plates in wear	6	6	6	1	1
Length	70.54	60.4	62.11		
Length wear surface	57.76	59.45	59.33	8.42	9.59
Width (widest plate)	43.44	40.68	39.63	51.74	52.43
Height (middle plate)			42.58	42.67	
Enamel thickness	1.73	1.84	2.14		2.39
Laminar frequency	10	9	9	6	6

Accession No.	**412**	**387**	**411**	**30189**
Tooth	LM^2	M?^{3}	RM^3	LM^3
No. plates	7+			
No. plates in wear	4			
Length				
Length wear surface	122.87			
Width (widest plate)	77.95	80.18E	77.69	85.42
Height (middle plate)	99.05			
Enamel thickness	2.9	3.34	5.42	4.24
Laminar frequency	5E4.5	4+	5.5	5

Accession No.	**EK 424**	**EK424**
Tooth	RM^3	LM^3
No. plates	10+	12
No. plates in wear	?	4
Length	269+	280
Length wear surface		128.11
Width (widest plate)	91	95.46
Height (middle plate)	112	120.06
Enamel thickness		5.15
Laminar frequency	5	5

and thick enamel. The rear of tooth is wider than the front.

Order Perissodactyla

Family Rhinocerotidae

The extant genera *Ceratotherium* Gray, 1867, and *Diceros* Gray, 1821, first appear in the late Miocene but at Lothagam are accompanied by the teleoceratine rhino *Brachypotherium* Roger, 1904 (Harris and Leakey, 2003b). Thus far, only the extant genera have been recovered from Kanapoi.

Ceratotherium Gray, 1867

Ceratotherium praecox Hooijer and Patterson, 1972

(Figure 14; Table 15)

KANAPOI MATERIAL. 30, Rt. nasal boss, occiput frag, and skull frags; 32, incomplete rami (Lt. and Rt. P$_3$–M$_3$); 33, Lt. mand frag (M$_2$); 36, skull (Lt. M$^{2–3}$, Rt. P^4–M^3) holotype; 38, Rt. P^4 frag, tooth frags; 538, dist Lt m/t III; 30187, partial skull (P$^{3–4}$); 30195, Lt. humerus; 30217, Lt. mand (P$_3$); 30554, Lt. P$_4$; 32556, Lt. dP/ frag; 32868, Lt. P$_4$.

Table 12 Kanapoi *Elephas ekorensis* lower teeth measurements

Accession No.	400	30169	411	30169	30170	30173	30175	32575
Tooth	LP$_2$	LP$_2$	LP$_3$	LP$_3$	LP$_3$	LP$_3$	LP$_3$	Lt. P$_3$
No. plates	4	4	6	6	6	6	5+	
No. plates in wear	none	2	6	1	none	6		5
Length	25.76	26.14	66.53+	68.1	62.66	70.33		5
Length wear surface	none	11.58	66.53	5.53	none	62.69		
Width (widest plate)	19.59	18.79		40.51	42.46	41.86	39.74	24.
Height (middle plate)	15.21			30.05	32.26			
Enamel thickness		0.97	1.6		2.79	1.71	1.97	2.3
Laminar frequency	20E	20E	9E	9E	9E	9E	10E	13
Accession No.		**28442**	**30175**	**30175**	**32575**	**409**	**26956**	
Tooth		Lt P$_4$	LP$_4$	RP$_4$	Lt. P$_4$	LM$_1$	RM$_1$	
No. plates		8	9	9	8+	8	7+	
No. plates in wear		8	5	5	3	1	3	
Length		68.6	113.2	116.95	106E	167E	120.46+	
Length wear surface			62.58	72.84	25	24.07	54.1	
Width (widest plate)		36.7	50.6	53.43		59.99	57.7	
Height (middle plate)						71.03	76.1	
Enamel thickness		2	2.5	2.57	2.5	3.61	2.72	
Laminar frequency		8		8	9E	6.5	6	
Accession No.			**30198**	**30639**	**30198**	**30639**		
Tooth			LM$_1$	Rt. M$_1$	LM$_2$	Lt. M$_2$		
No. plates				8		9x		
No. plates in wear			5+	8	3			
Length				135		179		
Length wear surface			96.13		54.19			
Width (widest plate)			63.51+	61				
Height (middle plate)						85		
Enamel thickness			3.41	3.56	4.13			
Laminar frequency			5E	6.5	5E	5		

Table 12 Continued

Accession No.	30236	30471	30625	38975
Tooth	Rt. M_3	LM_3	Lt. M_3	Rt. M_3
No. plates	8+	13	6+	7+
No. plates in wear		3		4
Length	223+	276		
Length wear surface		75.79		
Width (widest plate)		86.47	75	80+
Height (middle plate)	100	105.7	95e	
Enamel thickness	4.2	5.05	4.5	4
Laminar frequency	3.5	5	5	4.5

Ceratotherium praecox appears to have been the precursor of the extant white rhino. As diagnosed by Hooijer and Patterson (1972), the cranium differs from that of *C. simum* (Burchell, 1817) by the greater concavity of skull roof, cranium less extended posteriorly, occiput more vertically inclined; cheek teeth not as hypsodont, lophs and lophids not markedly oblique, anterointernal corners of upper teeth not rounded, no medifossettes in P^2–M^2 and no fossettids in lower cheek teeth, internal cingula in upper cheek teeth variable. *Ceratotherium praecox* has been recovered from throughout the Kanapoi sequence.

The holotype of *C. praecox* is a relatively complete cranium from Kanapoi (KP 36; Hooijer and Patterson, 1972) but the Kanapoi material is in general much less well preserved than the abundant material of this species that was subsequently described from Langebaanweg (Hooijer, 1972). Newly recovered material includes KP 30187, an incomplete cranium including part of the left maxilla with dP^{2-3}, part of the anterior cranial vault with anterior part of left zygomatic arch, and the occiput dorsal to the foramen magnum. The specimen displays primitive characters for *Ceratotherium* in that the occiput is still vertical and not backwardly inclined as in *C. simum,* the posterior part of the cranial vault is flat and rising upward as in *Diceros,* and although the length from the orbit to the nuchal crest cannot be measured because the bone is not continuous it was evidently much greater than in the Lothagam examples of *Diceros.* The premolar lophs are more transversely oriented than in the extant *C. simum.*

Diceros Gray, 1821

Diceros bicornis (Linnaeus)

(Figure 14; Table 16)

KANAPOI MATERIAL. 30216, Lt. P^2; 30472, Lt. P^3; 40, max frags (Lt. dP^3); 39, Rt. humerus.

As at most Pliocene and Pleistocene sites in sub-Saharan Africa, *Diceros* was not a common element of the Kanapoi biota but it is represented by several isolated teeth and a nearly complete right humerus. Older *Diceros* material has been recovered from the Upper Nawata and Apak Members at Lothagam.

The presence together of *Ceratotherium praecox* and *Diceros bicornis,* the latter being less common, is characteristic of Pliocene and early Pleistocene sites in East Africa. *Brachypotherium lewisi* Hooijer and Patterson, 1972, persists into the Apak Member at Lothagam but has not been found at Kanapoi or in the temporally equivalent Kaiyumung Member at Lothagam.

Family Equidae

Subfamily Equinae

Hipparionine horses of the genus *Hippotherium* von Meyer, 1829, first appear in Africa between 10 and

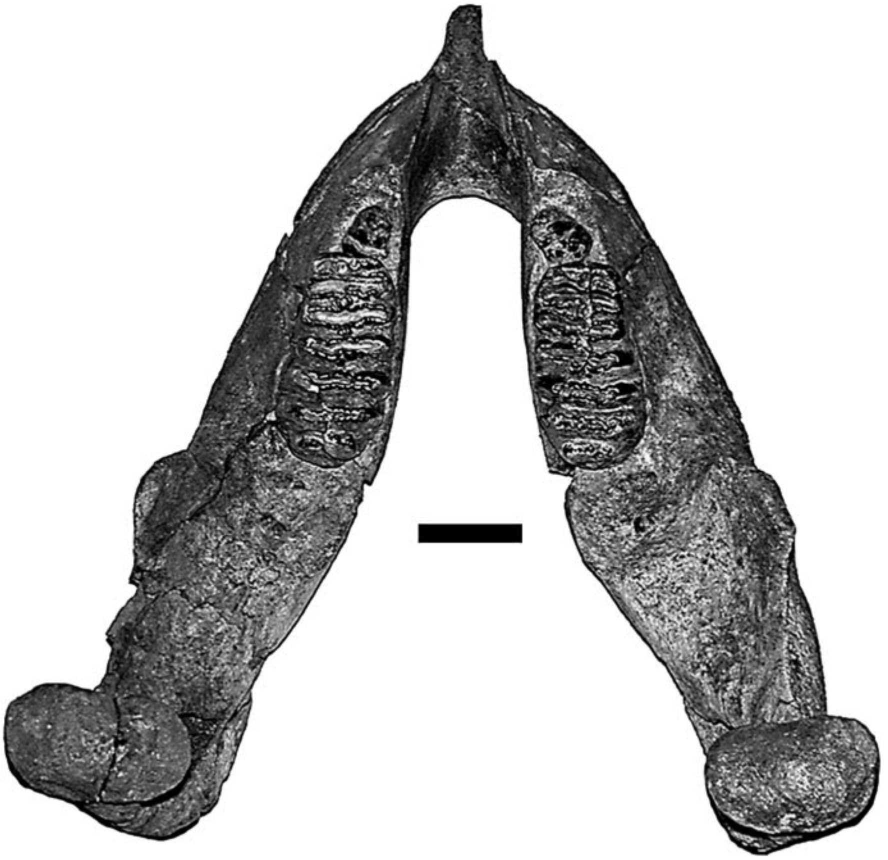

Figure 12 KNM-KP 30616; *Loxodonta adaurora* mandible with Lt. and Rt. P_3, P_4, occlusal view; scale = 5 cm

11 million years ago. A second wave of migration, this time of the genus *Eurygnathohippus* van Hoepen, 1930, took place about 7 million years ago (Bernor and Harris, 2003). Equid material retrieved from Kanapoi represents only the latter genus.

Eurygnathohippus van Hoepen, 1930

As pointed out by Bernor and Harris (2003), all African hipparions of the genus *Eurygnathohippus* are united by the synapomorphy of ectostylids on the permanent cheek teeth. Eurasian and North American hipparions lack this character except in extremely worn hipparion teeth from the late Miocene Dinotheriensandes locality of Germany. *Stylohipparion* van Hoepen, 1932, is the junior synonym of *Eurygnathohippus* by year priority.

Eurygnathohippus sp. indet.

(Tables 17, 18)

KANAPOI MATERIAL. 42, Rt. M_3; 43, Lt. P^2, P^4, M^1, Rt. P^2–M^3; 44, Lt. mandible frag (P_3–M_3); 45, m/t frag; 46, Rt. M^1 and tooth frags; 47, Lt. P^3, M^3; 48, Rt. M^1; 49, Lt. and Rt. M^{2-3}; 50, M frags; 51, Lt. P^3; 52, Lt. P_3 and /M frags; 53, Rt. P^3; 54, enamel frags; 55, Lt. M_2 and /M frag; 56, Lt. P_3; 57, Lt. P^3; 58, Lt. M_{1-2}; 470, M/ frag; 503, enamel frags; 508, magnum; 518, M frag; 532, Lt. mandible frags (P_{2-3}, M_{1-3}); 544, Lt. M^1; 30167, dist m/p; 30218, Lt. M^{1-2} and tooth frags; 30220, Rt. M^3; 30473, Rt. M^1 frag; 30476, Rt. P^2; 30493, *M* frags; 30555, Lt. P_3 and M_3; 30556, Rt. P^3–M^1; 30560, M/ frags; 32809, dI/.

Hooijer and Maglio (1974) recognized three equid species from Kanapoi and Lothagam that they identified as *Hipparion turkanense* Hooijer and Maglio, 1972, *H. primigenium* von Meyer, 1829, and *Hipparion* cf. *H. sitifense* Pomel, 1897. Bernor and Harris (2003) reviewed the Lothagam equids and recognized two common species from the Nawata Formation—*Eurygnathohippus turkanense* and the smaller *E. feibeli* Bernor and Harris, 2003. They also attributed a few postcranial elements to *Hippotherium* cf. *H. primigenium*. Bernor and Harris noted the great variation in tooth mor-phology in the equid teeth from Lothagam and recommended against naming Pliocene equids from East Africa that were younger in age

Table 13 Kanapoi *Loxodonta adaurora* upper teeth measurements

Accession No.	**30150**	**406**	**406**	**28441**	**383A**	
Tooth	RP^2	RM^1	RM^2	M^2	LM^3	
No. plates	3				9	
No. plates/wear	3				2	
Length	19.31				273	
Length wear surface	16.38			101		
Width (widest plate)	16.77	69.19	72.71		121	
Height (middle plate)					109	
Enamel thickness		4.83		3.5	5.27	
Laminar frequency	20E	5E	4.5	4	3.5	
Accession No.	**383B**	**383C**	**383E-J**	**385**	**385**	**389**
Tooth	RM^3	RM^3		RM^3	LM^3	M^3
No. plates	9	9	?9	10	10	
No. plates in wear	7	2	?6	8	8	
Length	238+	284		242	234	
Length wear surface	215+	96		189	185	
Width (widest plate)	119	116	110	105.6	108	
Height (middle plate)	94+	117				
Enamel thickness	4.51	4.48	4.48	4.69	4.42	4.23
Laminar frequency	3.5	4		3.5E	3.5	3.5
Accession No.	**390**	**390**	**30188**	**30191**	**30204**	
Tooth	RM^3	LM^3	RM^3	LM^3	LM^3	
No. plates	10		8		9+	
No. plates in wear	9		8		4+	
Length	287+		260	265+	250+	
Length wear surface	261+				125+	
Width (widest plate)	107+				110	
Height (middle plate)					91e	
Enamel thickness	6.22	4.03	3.54	7.02	4.18	
Laminar frequency	3.5	3.5	3.5	3.5	3.5	
Accession No.	**30204**	**30596**				
Tooth	RM^3	LM^3				
No. plates	9+	7+				
No. plates in wear	4+	7+				
Length	244+					
Length wear surface	130+					
Width (widest plate)	109	120				
Height (middle plate)	85e					
Enamel thickness	4.06	4.5				
Laminar frequency	4	3				

than the Nawata Formation until appropriately complete diagnostic material had become available. This recommendation seems pertinent for the Kanapoi equid hypodigm—given the complete absence of cranial material and that the majority of Kanapoi equids comprise isolated teeth or tooth fragments. A few specimens (KP 48, 51, 53, 57) seem a little larger than most while two specimens (KP 49, 30220) seem a little smaller, but it would be unwise to speculate whether such minor differences are meaningful taxonomically.

Order Artiodactyla

Family Hippopotamidae

The earliest known representatives of this family constitute teeth from middle and late Miocene sites in Kenya and Tunisia that are assigned to the genus *Kenyapotamus* Pickford, 1983. The extant representatives constitute the dwarf hippo *Hexaprotodon liberiensis* Morton, 1849, from West Africa and the common hippo *Hippopotamus amphibius* Linnaeus. *Hexaprotodon* is the first extant

Table 14 Kanapoi *Loxodonta adaurora* and *L. exoptata* lower teeth measurements

Accession No.	**30616**	**30616**	**381**	**381**	**391**	**406**
Tooth	RP_3	RP_4	LM_1	RM_1	LM_1	RM_1
No. plates	x2x	7	6+	6+	4+	5+
No. plates in wear		6	6+	6+		5+
Length	32.4					
Length wear surface		106				
Width (widest plate)	24.4	53.4	70.44	72.98	70	70
Height (middle plate)	17.5				66	
Enamel thickness		2.4	4.1	4.2	3.7	4
Laminar frequency		7	5	5	4.5	5

Accession No.	**396**	**403**	**406**	**32542**	**32542**
Tooth	RM^2	LM_2	RM_2	RM_2	LM_2
No. plates			6+	4+	4+
No. plates in wear		4+	1+	4+	4+
Length				89.36	96.75+
Length wear surface				89.34	96.74
Width (widest plate)	85.03	90.17	76	80.4	84.4
Height (middle plate)			81+		
Enamel thickness	4.25	5.81		4.18	5.55
Laminar frequency	4.5E	4	4.5	4	4

Accession No.	**385 (type)**	**385**	**403**	**407**
Tooth	LM_3	RM_3	LM_3	RM_3
No. plates	11	11		11
No. plates in wear	8	9		5
Length	279.4	276		289
Length wear surface	212.4	228		165
Width (widest plate)	103	100.4	93.37	100+
Height (middle plate)			98.92	101
Enamel thickness	4.39	5.12		3.73
Laminar frequency	4	3.5		4

Specimen No.	**30193**	**30654**	**30611 (=*L. exoptata*)**
Tooth	LM_3	RM_3	RM_2
No. plates	8+	11	8
No. plates in wear	7+	11	8
Length		295	173.6
Length wear surface			158E
Width (widest plate)	96	110	71.88
Height (middle plate)			
Enamel thickness	5.5	4.98	3.58
Laminar frequency	3.5	3.5	5

genus to occur in the fossil record. Two species have been documented by Weston (2003) from the late Miocene of Lothagam—*Hex. harvardi* Coryndon, 1977, and *Hex. lothagamensis* Weston, 2000. Neither persist into the early Pliocene of Kanapoi where two hippopotamid species are represented—*Hexaprotodon protamphibius* Arambourg, 1944, which is the common Pliocene hippo from the Lake Turkana Basin, and a smaller unnamed species.

Hexaprotodon Falconer and Cautley, 1836

Hexaprotodon protamphibius (Arambourg, 1944)

(Figure 15; Tables 19–21)

KANAPOI MATERIAL. 1, Rt. ramus and symphysis; 2, upper premolars; 3, Lt. glenoid; 4, /C frag; 5, mand frag (P_2); 6, Lt. and Rt. mand frags (M_{1-3}); 7, Rt. M_3; 8, symphysis and incomplete ramus; 9, C, I, foot bones; 10, Rt. C/; 11, max frag

Figure 13 KNM-KP 30611; *Loxodonta exoptata,* Rt. M_2, occlusal view; scale = 5 cm

(Lt. M^{2-3}); 12, Lt. radio-ulna; 13, distal humerus; 14, incomplete forelimb; 15, juvenile Rt. mand (/C, dP_4–M_1); 16, teeth frags; 17, astragalus; 18, Rt. femur; 20, atlas; 21, Rt. /C frag; 22, cranium; 23, ulna; 24, tusk frags and ramus; 25, C/; 26, M/ and skull frags; 27, P_3, M_1, roots dP_4 in ramus; 28, ramus frag (incomplete cheek teeth); 29, incomplete /M; 236, tooth frags; 288, Rt. scapula, ribs and vertebra frags; 289, cervical vertebra; 290, thoracic vertebra; 450, Lt. scapula frags; 456, Rt. /C; 543, m/p, phalanx; 560, mand; 8690, teeth frags; 8696, mand frags; 8700, femur and ulna frags; 8720, calcaneum and bone frags; 8751, 2nd phalanx; 8752, astragalus; 8753, astragalus; 9910, cranium (M^3 erupting); 30153, mid phalanx; 30209, Rt. M^2 lacking distal portion; 30210, Lt. M_3, tooth and tusk frags; 30211, Lt. M_2 broken distally; 30224, Rt. maxilla (M^{1-2}); 30414, astragalus, calcaneum and prox tibia; 30415, P^1; 30488, m/p; 30599, Rt. I_3; 30621, C/; 30632, Rt. M_1; 30638, cranium and mandible; 31737, phalanx (diseased); 32521, M_1; 37372, M_3, /I, /C.

Hexaprotodon protamphibius was diagnosed by Gèze (1980) as a hexaprotodont or tetraprotodont hippopotamus of medium or submedium size. The skull is relatively narrow with widely separated canine alveoli and orbits little elevated above the facial plane. The lacrimals are enlarged anteriorly and generally separated from the nasals by the persistence of an antorbital process of the frontal. Anterior teeth are small with incisors closely spaced anteriorly; upper canines with deep posterior longitudinal groove; lower canines compressed laterally with finely striated enamel and subparallel

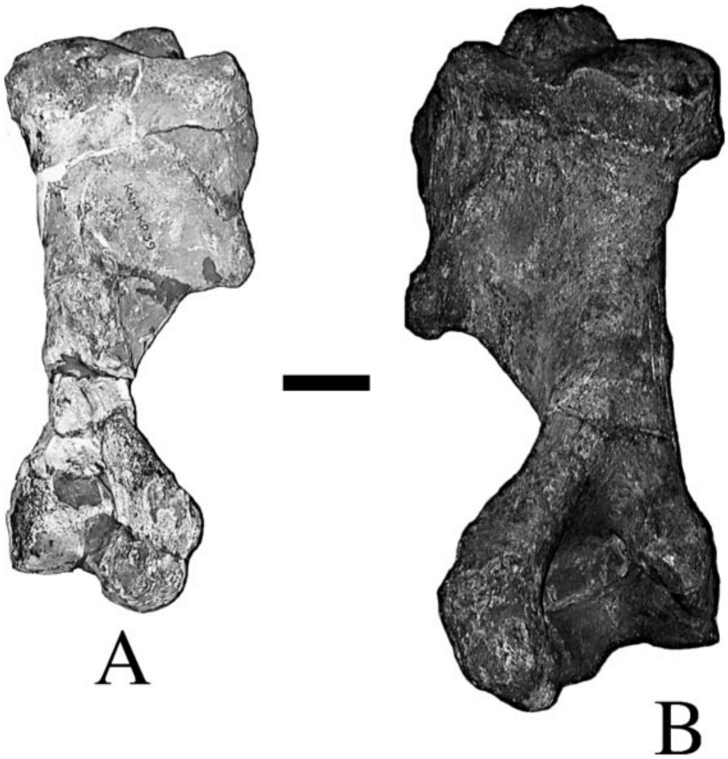

Figure 14 **A** = KNM-KP 39, *Diceros bicornis* right humerus; **B** = KNM-KP 30195, *Ceratotherium praecox* left humerus, posterior view; scale = 5 cm

Table 15 **Kanapoi *Ceratotherium praecox* teeth measurements**

Upper	30187	Lower	30217	30554	32868	LT 32L	LT 32R
P^1 ap		P_1 ap					
ant tr		ant tr					
post tr		post tr					
P_2 ap		P^2 ap					
ant tr		ant tr					
post tr		post tr					
P^3 ap		P_3 ap	40.58			36.69	
ant tr		ant tr	26.74			26.31	
post tr	46.47	post tr				29.01	
P^4 ap	48.98	P_4 ap		46.15	45.69	48E	
ant tr	54.88	ant tr		30.98	28.95	31+	
post tr		post tr		32.11		27.62	
M^1 ap		M_1 ap				46.62	
ant tr		ant tr				33.08	
post tr		post tr				33.66	30.78
M^2 ap		M_2ap				34.41	31.32
post tr		post tr				30.93	32.46
M^3 ap		M_3 ap					
ant tr		ant tr					
post tr		post tr					

Table 16 Kanapoi *Diceros bicornis* tooth measurements

		41	30216	30472
P^1	ap	18.94		
	ant tr	21.83		
	post tr			
P^2	ap	29.6	36.04	
	ant tr	33.98	39.37	
	post tr	38.33	41.59	
P^3	ap	36.17		
	ant tr	44.29+		57.23
	post tr	48.23		55.78

Table 17 Kanapoi *Eurygnathohippus* sp. indet. upper dentition measurements

		43	46	47	48	49
P^2	ap	35				
	tr	23.6				
P^3	ap	24.2				
	tr	28.1		27.1		
P^4	ap	22.9				
	tr	28.3				
M^1	ap	22.9	24.5		28.1	
	tr	25	23.7		28.8	
M^2	ap	22.9				20.5
	tr	24.2				19.5+
M^3	ap	23.4		23.8		20.2
	tr	22.1		21.3		18.4

		51	53	57	544
P^2	ap				
	tr				
P^3	ap	26.7	31.3	28.5	
	tr	25	25.2+	25+	
P^4	ap				
	tr				
M^1	ap				25.6
	tr				21.5
M^2	ap				
	tr				
M^3	ap				
	tr				

		30218	30220	30473	30476	30556
P^2	ap				36.9	
	tr				25.8	
P^3	ap					24.4
	tr					24.2
P^4	ap					21.8
	tr					23.4
M^1	ap	23.9		23.6		22.9
	tr					18.8
M^2	ap	23.4				
	tr					
M^3	ap		20.3			
	tr		20			

Table 18 Kanapoi *Eurygnathohippus* sp. indet. lower dentition measurements

		42	44	52	55	56
P_2	ap					
	tr					
P_3	ap		27.3	26		25.8
	tr		16.8	16.1		18.6
P_4	ap		26.7			
	tr		16.2			
M_1	ap		24.3			
	tr		15.4			
M_2	ap		25.7		25	
	tr		14.7		15.2	
M_3	ap	25.2				
	tr	10.4				

		58	532	30555
P_2	ap		32.1	
	tr		15.1	
P_3	ap			29.3
	tr		15.8	17.9
P_4	ap			
	tr			
M_1	ap	23.5	27.4	
	tr	13.3	14.9	
M_2	ap	25.6	26.9	
	tr	12.4	15	
M_3	ap		27.9	28
	tr		12	12

ridges. Cheek teeth are aligned in subparallel rows, brachyodont; premolars simple and with few pustules, lower premolars often with a linguodistal stylid; quadricuspate molars with poorly developed trefoils; simple cingulum sometimes bears styles or stylids. Facial region of the skull is larger than cranial region. The mandible is massive, longer than wide, with horizontal rami incurved beneath the premolars. Limb bones are relatively elongate, articular surfaces more rounded and interarticular crests more salient than in *Hippopotamus amphibius*.

The common hippo at Kanapoi is a small hexaprotodont form of comparable size to *Hexaprotodon protamphibius* from the lower members of the Koobi Fora Formation (Harris, 1991a). Coryndon (1977) assigned Kanapoi hippo material collected by the Harvard University expeditions to *Hexaprotodon harvardi*, but Weston (1997) compared this material to *Hex. protamphibius* and noted the similarity of the Kanapoi specimens both to those from the early part of the Koobi Fora Formation and to those from the lower part of the Shungura Formation that Gèze (1985) had assigned to *Hex. protamphibius turkanensis* (Boisserie, 2002). *Hexaprotodon protamphibius* differs from the earlier *Hex. harvardi* from the Nawata

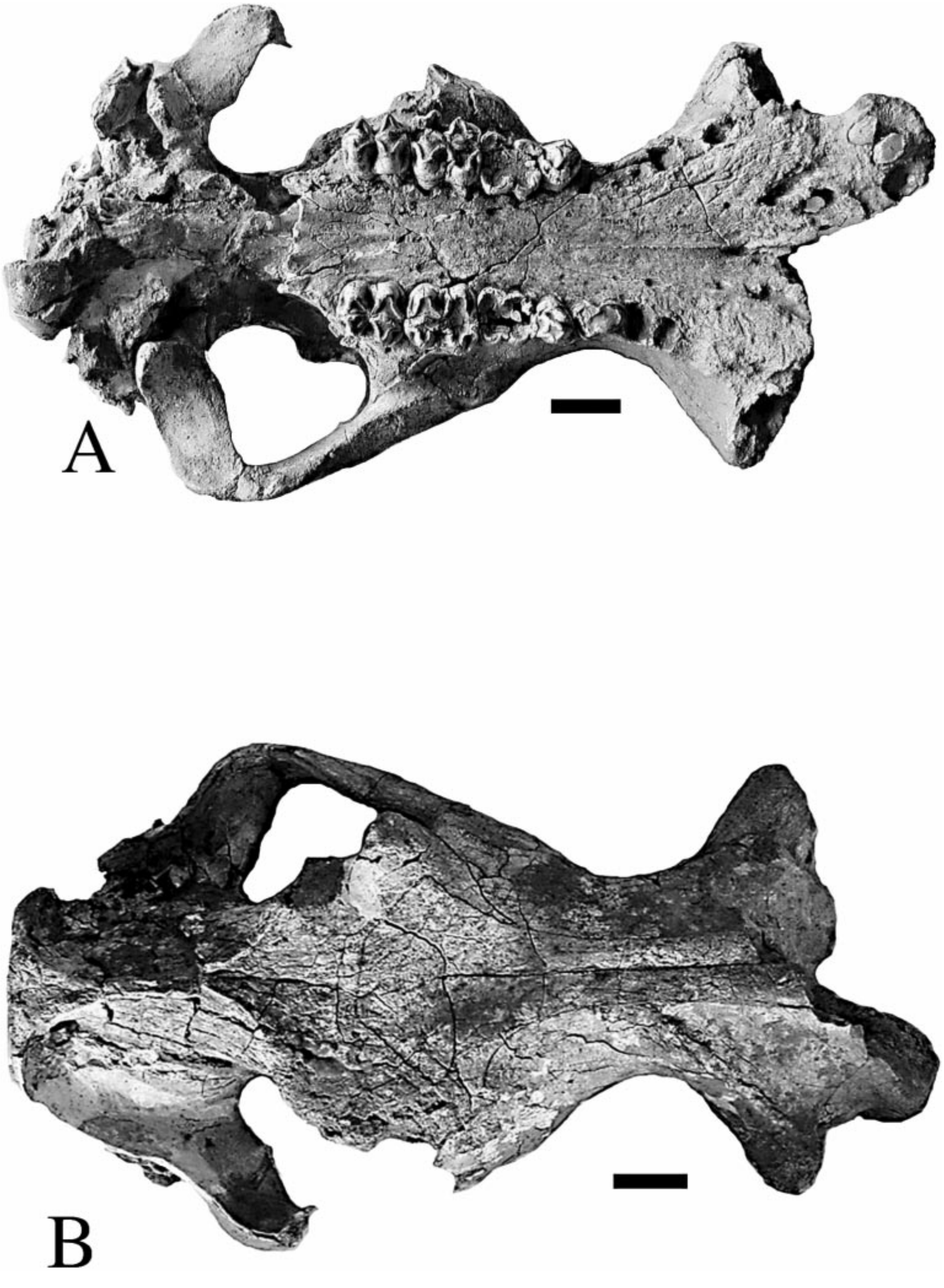

Figure 15 KNM-KP 22; *Hexaprotodon protamphibius* cranium; **A** = occlusal view; **B** = dorsal view; scales = 5 cm

Formation and Apak Member of Lothagam because of the size differentiation between the first and posterior incisors (in *Hex. harvardi*, they are of equal size) and by its shorter, stockier limbs (*Hex. harvardi* limbs are larger but more gracile) (Weston 2003). The basicranium is similar to that of *Hex. harvardi* and the cheek teeth are of comparable size but the occiput is less tall and the palate is wider; the mandible of *Hex. protamphibius* differs from that of *Hex. harvardi* in that the symphysis is longer and wider but less tall and that the tooth row is narrower (Boisserie, 2002).

Table 19 Kanapoi *Hexaprotodon* cf. *H. protamphibius* skull measurements

	22	30638
Length C/ to occipital condyle	560	570
Width at canines	304	330e
Width at P^4	141	125
Zygomatic width	373	370

Table 20 Kanapoi *Hexaprotodon* cf. *H. protamphibius* upper teeth measurements

		2	11	22L	22R
I^2	ap			16.7	
	tr			20e	
I^3	ap			16.4e	
	tr			18e	
P^2	ap	45e			
	tr				
P^3	ap	41e		38	
	tr	29.9		25.6	
P^4	ap			35	32
	tr			30.6	31.7
M^1	ap				
	tr				
M^2	ap		46.8e	50	52e
	tr			47.6	50e
M^3	ap		47.8	47	47
	tr		46.7	45.9	45

		26L	26R	9910	30209	30224
P^2	ap		41.1			
	tr					
P^3	ap		38e			
	tr					
P^4	ap	30				
	tr	32.6e				
M^1	ap					38.4
	tr					40e
M^2	ap	48.7		47.4	45.5	49
	tr	49		48		48.3
M^3	ap	46.7	45.1			
	tr	47.8	47.8			

		30415	30638L	30638R
P^1	ap	26.2		
	tr	17		
P^2	ap		39.9	
	tr		32	
P^3	ap		39.7	39e
	tr		31.8	
P^4	ap		34	33.2
	tr		32.1	32.7
M^1	ap		44.4	46.3
	tr		39	37.8
M^2	ap		50.5	53.5
	tr		46.8	46.2
M^3	ap		51.5	52.1
	tr		46.4	47.3

Hexaprotodon cf. *Hex. protamphibius* has been recognized from the Apak Member of the Nachukui Formation (Weston, 2003) and *Hex. protamphibius* persists into the Kalochoro Member of the Nachukui Formation (Harris et al., 1988). It is likely that *Hex. protamphibius* gave rise to *Hex. karumensis* Coryndon, 1977, that dominated the latest Pliocene and early Pleistocene aquatic habitats of the Lake Turkana Basin (Harris, 1991a), an interpretation supported by the phylogenetic analysis of Boisserie (2002).

Hexaprotodon sp. indet.

(Figure 16; Table 22)

KANAPOI MATERIAL. 30552, Lt. max with P^2–M^3.

One maxilla has teeth that are appreciably smaller than the material attributed to *Hexaprotodon protamphibius* but by itself is insufficient to determine whether this is *Hippopotamus imagunculus* Hopwod, 1926, the small hippo common to the Western Rift, or a progenitor of *Hexaprotodon aethiopicus* (Coryndon and Coppens, 1975) the small species present in Plio–Pleistocene horizons in then northern Turkana Basin, or an entirely new species.

Family Suidae

Genera of the suid subfamilies Hyotheriinae, Listriodontinae, and Sanitheriinae predominated in the early and middle Miocene of sub-Saharan Africa but in the late Miocene were replaced by tetraconodontine immigrants from Asia. *Nyanzachoerus* Leakey, 1958, and the more hypsodont *Notochoerus* Broom, 1925, were characteristic tetraconodontine genera of the latest Miocene and early Pliocene of sub-Saharan Africa. These two genera persist into late Pliocene localities, where they are joined by a second wave of Asian immigrants comprising the suine genera *Kolpochoerus* van Hoepen and van Hoepen, 1932, *Metridiochoerus* and *Potamochoerus* Gray, 1854. The last three genera are not present at Kanapoi.

Nyanzachoerus Leakey, 1958

Nyanzachoerus, as diagnosed by Cooke and Ewer, 1972, and Harris and White, 1979, is a tetraconodontine genus that evidently migrated to Africa from Asia during the late Miocene. Nyanzachoere cheek teeth are similar to those of the extant *Potamochoerus* in basic structure but tending to be more hypsodont and with main cusps of molars distinctly more columnar. The third and fourth premolars are relatively larger than in *Potamochoerus.* The upper canines are oval to flattened oval in transverse section, the lower canines verrucose with thin, weakly grooved enamel on two lateral faces. Strong sexual dimorphism is expressed by the size

Table 21 Kanapoi *Hexaprotodon* cf. *H. protamphibius* lower teeth measurements

		1	6R	6L	7	15
I_i	ap	25				
	tr	25.4				
I_2	ap	16.1				
	tr					
I_3	ap	19.4				
	tr	20e				
/C	ap	38				
	tr	58				
P_1	ap					
	tr					
P_2	ap	33.4e				
	tr					
M_1	ap		48.8	48.4		46.7
	tr		34.9	36		33
M_2	ap	50.7		55		
	tr			43.9		
M_3	ap	63e			70e	
	tr	37e			37.3	
dP_4	ap					
	tr					24.8
		27	**30210**	**30211**		
P_2	ap					
	tr					
P_3	ap					
	tr					
P_4	ap					
	tr					
M_1	ap	46.5				
	tr	35.4				
M_2	ap					
	tr					
M_3	ap		62.7			
	tr		37	34.5e		
		30599	**30632**	**30638L**	**30638R**	**32521**
I_i	ap			27	27.5	
	tr			25	25.5	
I_2	ap			21.5		
	tr			19.7		
I_3	ap	20.6		23		
	tr	21.4		21.7		
/C	ap					
	tr					
P_1	ap					
	tr					
P_2	ap			35.5	36.9e	
	tr			20.1	20	
P_3	ap			37		
	tr			23.1		
P_4	ap			38.9	36.7	
	tr			27	26.9	
M_1	ap		47	48	49.5	
	tr		35		34.9	
M_2	ap			52	51.5	50.5
	tr			38	36.5	35.7
M_3	ap			64	63.5	
	tr			36.9	35.8	

of canines and massiveness of skull. Hollow bony protuberances or bosses are present on the zygomatic arches in males but weak or absent in females. The corpus of the mandible is heavy and contrasts markedly with the unusually thin bone forming the angle.

Nyanzachoerus pattersoni
Cooke and Ewer, 1972

(Figures 17, 18; Tables 24–26)

KANAPOI MATERIAL. 201, Rt. P^2–M^3; 202, Rt. M_3 broken; 205, Rt. M_1 and M_2; 206, partial Rt. M^2; 213, partial Lt. mand (Lt. P_3–M_2, M_3 erupting); 214, frag Lt. max (Lt. P^{3-4}); 215, skeletal elements and tooth frags; 218, Rt. mandible frag (P_{3-4}, M_3 frag; 219, Rt. M_2; 220, broken mand, teeth worn; 221, partial Lt. and Rt. mand rami (milk teeth and Rt. M_1); 222, frag Rt. max (dP^4, partial M^1); 223, partial skull (Lt. P^4, M^3, Rt. M^3); 228, Rt. M_1; 231, facial frag of old male; 232, Rt. M_3 tooth frags; 238, Rt. M_3; 239, female skull and mand (holotype); 240, Lt. and Rt. mand and teeth; 244, subadult skull; 249, mand symph; 255, Lt. mand (Lt. P_4–M_2); 256, Rt. mand (P_4–M_3); 258, mand (Lt. P_4–M_3); 259, Lt. mand (M_2 and M_3); 260, Rt. M^2; 261, frag M^3, C; 262, skull and mand frags; 263, Lt. and Rt. mand (Lt. P_3–M_3); 264, broken skull and mand (M_3); 266, Lt. juv mand (C, dP_2, M_{1-2}); 273, M^3; 275, Lt. mand (P_4–M_3); 329, female cranium and mandible, atlas vertebra, thoracic vertebra; 533, mand frag (M_3); 534, Lt. M_3; 18566, partial skull (Lt. P^3–M^2); 30159, Rt. P^4 and M^1 and tooth frags; 30160, female mand (Lt. and Rt. I_{1-2}, C, Rt. P_2–M_3); 30161, male mand (Rt. P_4, M_3, roots Lt. and Rt. I_1-/C Rt. P_2, P_4–M_1); 30162, male max (P^{2-4}); 30165, male Lt. and Rt. C/, worn *M* frag, I^2; 30166, Rt. mand (broken M_3), Lt. P_4, condyle, partial M^3; 30168, Rt. mand (P_{2-3}); 30177, female mand and symphysis (Lt. and Rt. I_{1-3}, Lt. P_{2-3}, M_{2-3}, Rt. P_{2-4}); 30179, mand (broken M_{2-3}); 30181, M_3 lacking talonid; 30183, mand (M_{2-3}), and frags symphysis; 30186, male cranium; 30203, male mand, skull and tooth frags; 30205, female symphysis (Lt. I_{1-2}), Rt. P_3, P_4; 30267, Lt. and Rt. male mand and symphysis (Rt. /C–M_3, Lt. P_3–M_3); 30268, male broken max and premax (Lt. and Rt. M^3); 30271, very broken male skull and teeth; 30403, Rt. mand frag (M_3 and roots M_2); 30409, Lt. mandible (P_4, roots M_1, M_{2-3}), tusk and mand frag; 30410, mand and broken teeth and dist tibia frag; 30411, M^3 talonid; 30413, DP^4 and M^1 and bone frags; 30430, Lt. max (P^4–M^2); 30433, partial skull and teeth; 30453, Rt P^{3-4}; 30456, M_2; 30458, Lt. M_2; 30462, Rt. M_2; 30474, upper teeth (Rt. P^4, partial M^1, M^2, M^3); 30475, Lt. mand (P_3–M_2), tooth frags; 30543, molar frags; 30545, I_3; 30547, Lt. mand (dP_4, M_{1-2}); 30551, Rt. mand frags (M_3); 30553, Lt. mand (P_3–M_2), Rt. mand (P_3–M_3) and frags; 30615, P^3; 30620, Male Rt. mand (P_4–M_3); 32515, Rt. M^3 and tooth frags; 32530, P_2; 32539, Rt. mand (P_4–M_3); 32553, Rt. I_2; 32802, mand (Rt.

Figure 16 KNM-KP 30552; *Hexaprotodon* sp. indet. left maxilla with P^2–M^3, occlusal view; scale 5 cm

P$_3$–M$_3$); 36841, broken mand (partial P$_3$, M$_1$, M$_2$, M$_3$) and opp P; 38978, male mandible Rt. /C–M$_3$, Lt. /C–P$_3$.

Nyanzachoerus pattersoni is a sexually dimorphic nyanzachoere that is larger than the late Miocene *Ny. syrticus* (Leonardi, 1952) from Lothagam and Sahabi. The first premolars are vestigial or absent. The third and fourth premolars are robust compared with those of *Ny. syrticus* subspecies but are relatively smaller, and the third molars are more elongate and with a more complex talon (id) (Harris and White, 1979). M$_3$ length is between 48 and 60 mm (van der Made, 1999). The holotype is a female skull from Kanapoi (KNM-KP 239).

Nyanzachoerus pattersoni is the common suid at Kanapoi. Harris and White (1979) interpreted *Ny. pattersoni* as a junior synonym of *Nyanzachoerus kanamensis* Leakey, 1958, but we now consider *Ny. kanamensis* to be a species with narrow premolars whose distribution was limited to the Western Rift (Harris and Leakey, 2003c). The teeth of *Ny. pattersoni* may be distinguished from those of *Ny. syrticus* and *Ny. devauxi* (Arambourg, 1968) by their larger size, more complex third molar talon(id)s, and proportionately smaller premolars. The third molars are shorter and have less complex talon(id)s than those formerly assigned to "*Nyanzachoerus*" *jaegeri* Coppens, 1971.The teeth display considerable size variation, polarizing between larger male and smaller female specimens. The larger male teeth are only slightly smaller than those of *Ny. australis* Cooke and Hendey, 1992, from Langebaanweg, but we think the variation seen in the Kanapoi sample reflects sexual dimorphism rather than the presence of two dentally similar species.

Table 22 Kanapoi *Hexaprotodon* sp. upper teeth measurements

		30552
P^2	ap	28
	tr	>22
P^3	ap	31
	tr	25
P^4	ap	22
	tr	23.5
M^1	ap	34
	tr	33
M^2	ap	39.7
	tr	41.1
M^3	ap	42.6
	tr	

The mandible of *Nyanzachoerus pattersoni* is robustly constructed. The symphysis is relatively narrow across the canine alveoli and moderately concave. The anterior border, which bears three pairs of well-developed and closely proximate incisors, is arched and projects in front of the canines. The concave superior symphysial surface is deeply excavated in front of the posterior border. The relatively small but stout canines are set at an oblique rather vertical angle. The inferior surface is smooth and only slightly flattened toward the incisive alveoli. The mandible constricts to its minimum width midway along the relatively short postcanine diastema. The posteroventral border merges smoothly with the inferior body of the corpus, which is short, robust, and becomes gradually deeper posteriorly.

At Lothagam, *Nyanzachoerus syrticus* and the much smaller *Ny. devauxi* predominate in the Nawata Formation. The more progressive *Ny. pattersoni* has not been recovered from strata earlier than the Kaiyumung Member although the dentally sim-

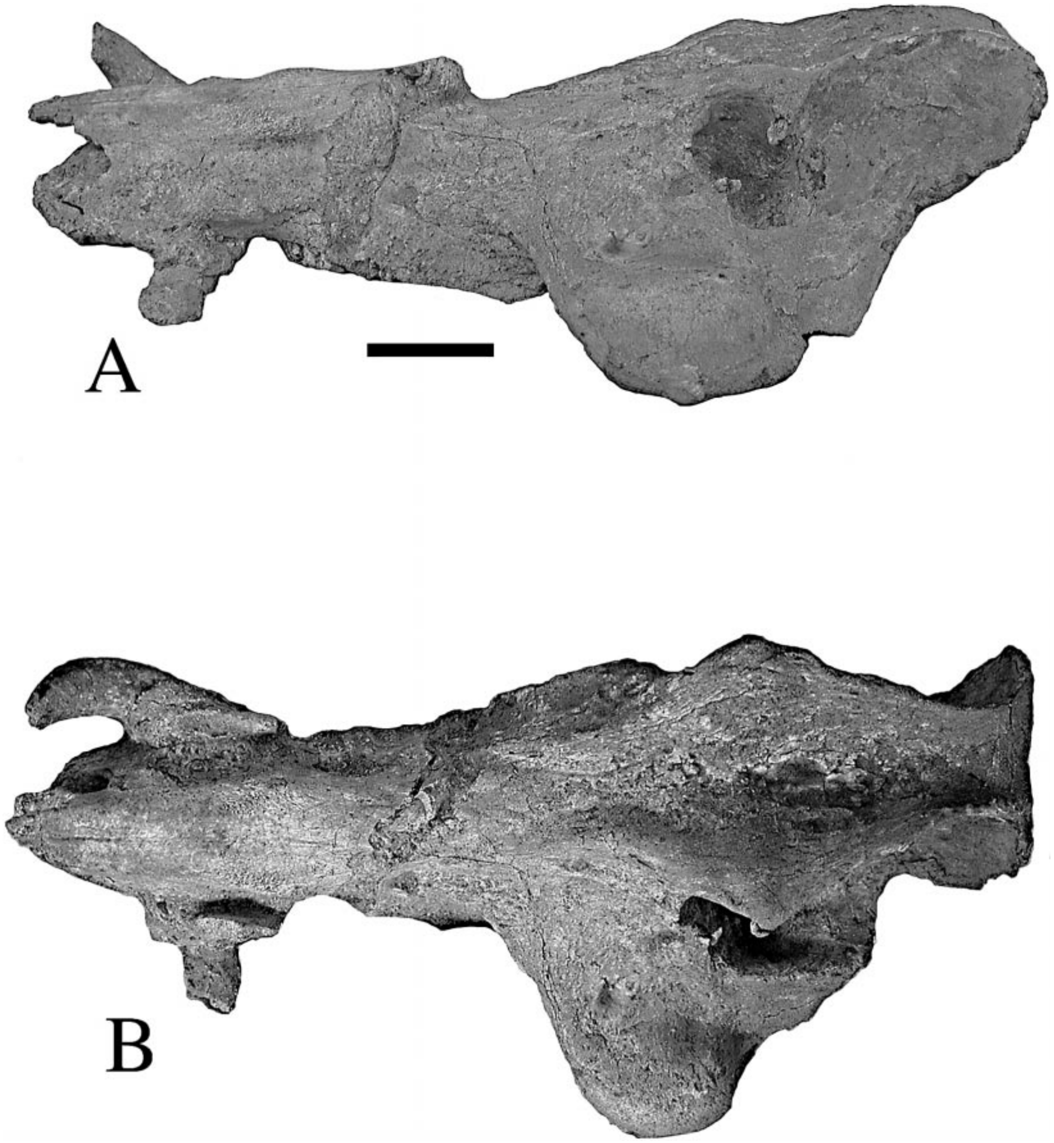

Figure 17 KNM-KP 30186, *Nyanzachoerus pattersoni*, cranium; **A** = left lateral view; **B** = dorsal view; **C** = anterior view. Scale = 5 cm

ilar but somewhat larger *Ny. australis* (Cooke and Hendey, 1992) occurs in the Upper Nawata and Apak Members.

Notochoerus Broom, 1925

Notochoerus species are tetraconodontines that have wide and flat mandibular symphyses, small premolars, elongate molars, and very long and hypsodont third molars. The M_3 is the longest of all tetraconodontines (van der Made, 1999).

Notochoerus jaegeri (Coppens, 1971)

(Figures 19, 20; Tables 24, 27, 28)

KANAPOI MATERIAL. 203, C/ frag; 225, broken Rt. M^3 and partial Lt. M^3; 209, partial M_3; 210, frag Rt. mand (M_3 broken); 211, Lt. M^3; 226, damaged mand (broken Rt. M_3 and P_3); 234, Lt. M^3, frag Rt. M^3; 235, mand (Lt. M_3, broken Rt. P_4 and /C); 241, damaged mandible (Rt. P_3); 242, male skull frags (zygomatic knob); 245, partial M_3; 251, partial skull and mand; 252, upper female canines; 253, Lt. M^3; 254, Rt. M_3 and tooth frags; 257, partial skull (Lt. and Rt. P^3–M^3); 265, M^3

Figure 17 Continued

frags; 267, mand; 269, juv mand (dP$_{3-4}$, M$_1$); 270, Lt. M$_3$; 26944, Rt. M^3 and tooth frags; 30178, large mand (Lt. /C, Rt. I$_{1-3}$, Lt. and Rt. P$_3$–M$_3$); 30180, Lt. mand (P$_3$–M$_3$); 30182, Lt. M$_2$, Rt. M$_2$; 30185, tusk frags; 30402, mand (M$_{2-3}$); 30452, mand (Rt. and Lt. /C–M$_3$); 30484, M^3 talon; 30550, mand (M$_{2-3}$); 30617, male skull (Rt. P^3–M^3); 32528, M$_{1-3}$; 32801, Lt. mand. frag (M$_3$).

Notochoerus jaegeri is a large progressive tetraconodontine possessing three pairs of premolars, of which the third and fourth are proportionately smaller than *Ny. syrticus* or *Ny. pattersoni.* The third molar is longer and taller and has more pillars than those of either of the latter taxa. There is a tendency for the molar enamel to be folded. The cranium and mandible are larger and more elongate than in *Nyanzachoerus* species; strong sexual dimorphism is evident, with the zygomatic swellings more localized but more protuberant in males (after Harris and White, 1979).

Cooke and Ewer (1972) assigned cranial and dental material of a large suid from Kanapoi and Lothagam to their new species *Nyanzachoerus plicatus,* but this taxon proved to be a junior synonym of the species *Nyanzachoerus jaegeri* erected by Coppens in 1971 for suid dentitions from Chad. Known mainly from its teeth, this species was interpreted by Harris and White (1979) to be morphologically and phylogeneticaly intermediate between, on one hand, nyanzachoeres represented by

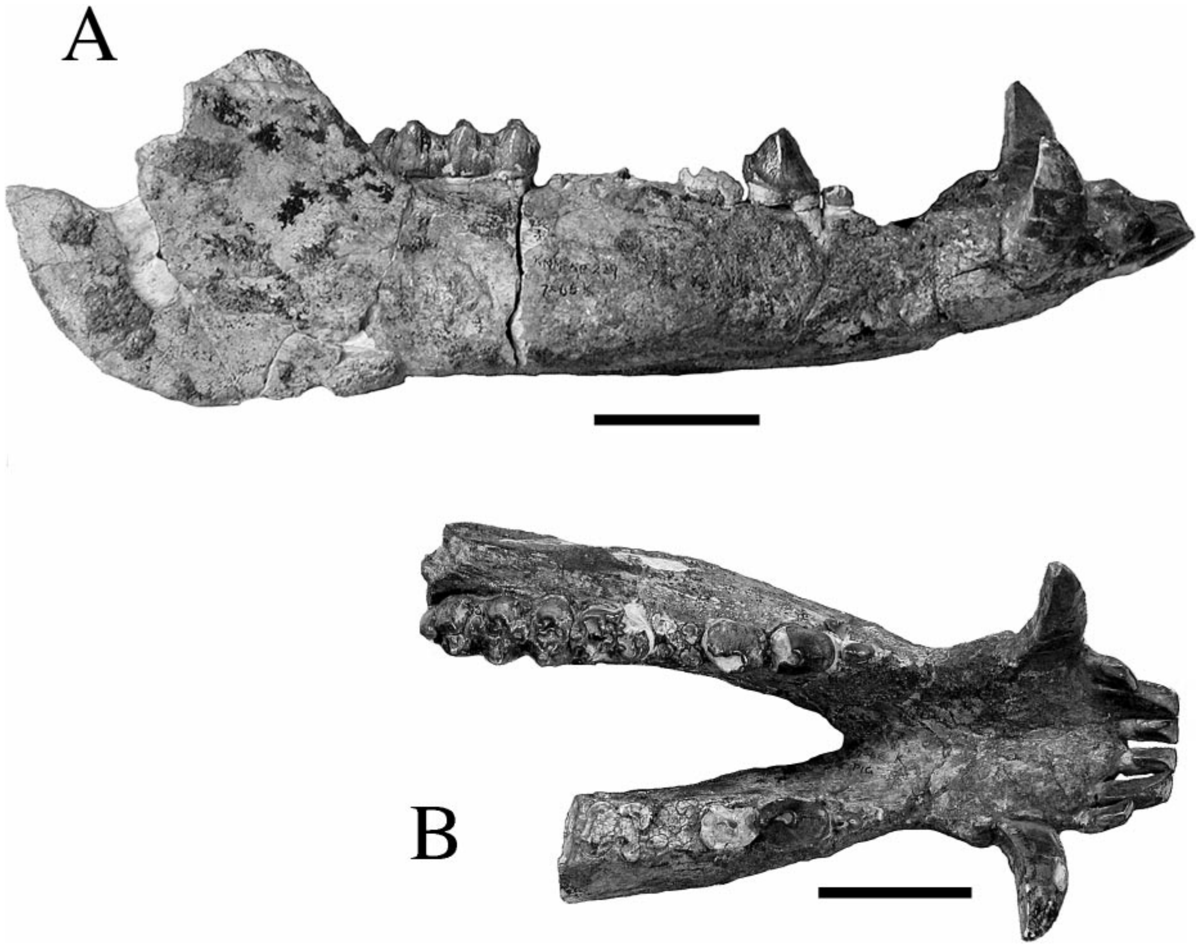

Figure 18 KNM-KP 239, *Nyanzachoerus pattersoni*, mandible; **A** = right lateral view; **B** = occlusal view; scales = 5 cm

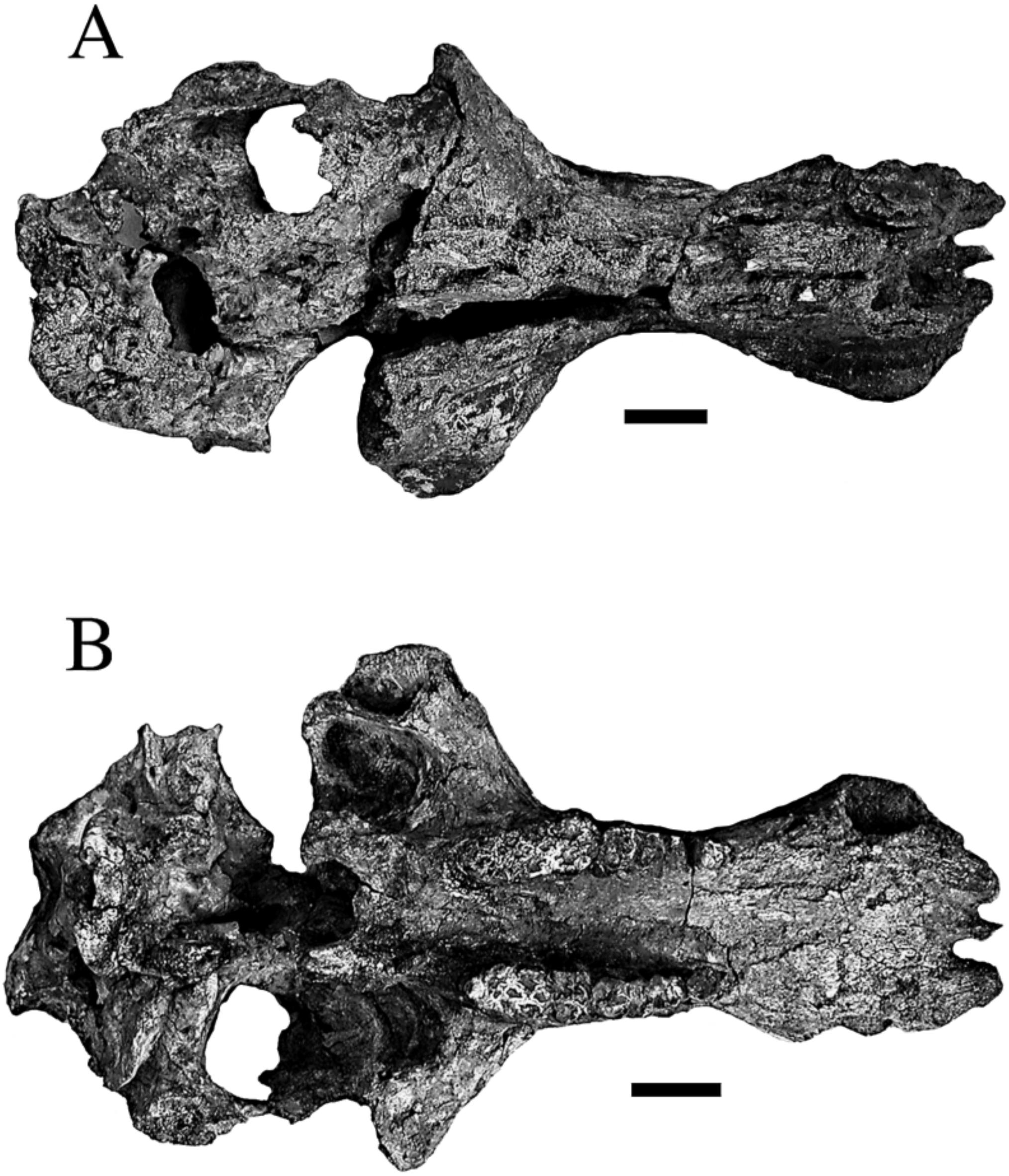

Figure 19 KNM-KP 30617, *Notochoerus jaegeri*, cranium; **A** = dorsal view; **B** = occlusal view; scales = 5 cm

Ny. kanamensis and *Ny. pattersoni* and, on the other, the somewhat younger notochoeres represented by *Notochoerus capensis* Broom, 1925, from South Africa and *Not. euilus* (Hopwood, 1926), from eastern Africa. New mandibles recovered from Kanapoi by National Museums of Kenya expeditions have augmented our understanding of this species and clarified its phylogenetic relationships.

In contrast with the relatively narrow mandibular symphyses of *Ny. pattersoni* and *Ny. syrticus,* that of *Notochoerus jaegeri* resembles the mandibular symphysis of *Notochoerus euilus* in its breadth and flatness. The corpus of the *Not. jaegeri* mandible is longer and less robustly constructed than that of either *Ny. pattersoni* or *Ny. syrticus*. The symphysis is distinctly spatulate and flattened at the widest point across the canine alveoli. The anterior border, which carries three pairs of rather small but well-spaced incisors is almost straight and thickened ventrally at the alveolus. It projects only slightly in front of the anterior edges of the canine alveoli. Behind the canines, the superior surface is less deeply excavated. The large heavy canines extend laterally and anteriorly from their alveoli at a more horizontal angle, curving posteriorly in their distal portions. The inferior surface thins anteriorly

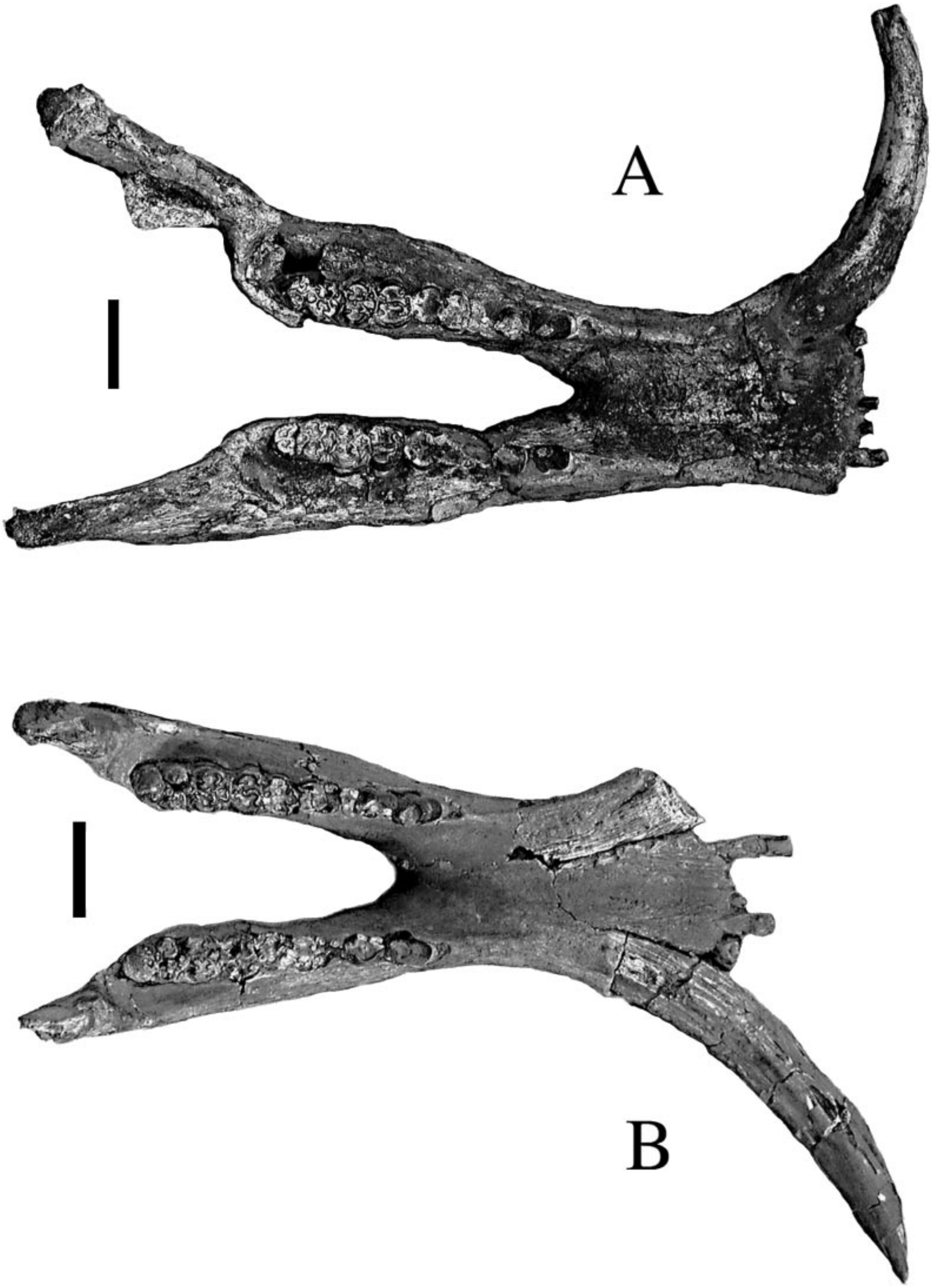

Figure 20 *Notochoerus jaegeri*, mandibles; **A** = KNM-KP 30178, occlusal view; **B** = KNM-KP 30452, occlusal view; scales = 5 cm

toward the incisor alveoli and between this and the canines is shallowly excavated either side of the midline. The posteroventral border projects below the inferior surface of the corpus. Posterior to the canines, the mandible constricts to its minimum width midway along the rather long postcanine diastema. The corpus is long, narrow, and relatively lightly built. The inferior surface is elevated between the posterior edge of the symphysis and the angle of the ramus.

The teeth of *Not. jaegeri* resemble a progressive version of *Ny. kanamensis* and *Ny. australis* teeth: the premolars have similar morphology but are proportionately smaller, the molars have similar morphology but the talon(id) of the third molar is more complex. However, the similarity of the orientation of the lower canines and the mandibular morphology to that of *Not. euilus* argues for incorporation of this species in *Notochoerus* rather than *Nyanzachoerus*.

Harris and White (1979) noted tetraconodontine upper third molars from Laetoli that they interpreted as primitive for *Not. euilus* on account of their larger size and more massive appearance. Recomparison of the Laetoli suids with those from Kanapoi suggests that the massive upper molars from Laetoli are better attributed to *Not. jaegeri* than to *Not. euilus*. *Notochoerus jaegeri* is also present in the Apak Member at Lothagam (Harris and Leakey, 2003c).

Notochoerus euilus (Hopwood, 1926)

Notochoerus euilus is a species of *Notochoerus* with a deep and narrow cranium bearing sexually dimorphic zygomatic knobs. The M^3 has two strong lingual talon pillars. The M_3 typically has three pairs of talonid pillars plus single midline terminal pillar or series of pillars. Individual major lateral pillars of molars are moderately tall, widely separated from adjacent lateral pillars, and taper sharply from their bases (Harris and White, 1979).

Table 23 Kanapoi Suidae cranial measurements

	Nyanzachoerus pattersoni 30186 M	*Notochoerus jaegeri* 30617
Width canine flanges	136	110.3
Width canine alveoli	160	
Nasal boss width	70	
Bizygomatic width	400	
Width postorbital processes	140	
Max width occiput	136	
Nuchal crest-foramen magnum	185	133+
Bicondylar width	76	98.5

Table 24 Kanapoi Suidae mandible measurements

	Nyanzachoerus mandibles				
	***N. pattersoni* M** **220**	***N. pattersoni*** **239**	***N. pattersoni*** **30161**	***N. pattersoni*** **30410**	***N. pattersoni*** **38978**
Length symphysis	144+	118	124	126	140+
Width at canines		75	77.7		110+
Width at I_3	76	61	62		78+
Length P_3–M_3	153	138	149.6	157	145
Length $P_{3–4}$	48.3	44.6	51.8	48.6	44
Min width diastema	73	55	52.8	60.2	63
	Notochoerus mandibles				
	***N. euilus* M** **ER3540**	***N. euilus* F** **KP30184**	***N. jaegeri* M** **KP226**	***N. jaegeri* M** **KP30178**	***N. jaegeri* M** **KP30452**
Length symphysis	172	131	189	195	185+
Width at canines	164	103+	178	150.5	148
Width at I_3	85		120.4	88.6	82
Length P_3–M_3	159	173		180	163
Length $P_{3–4}$	36	44		46.7	45.2
Min width diastema	63	68	78	85	74

Table 25 Kanapoi *Nyanzachoerus pattersoni* upper tooth measurements

		201R	205R	205L	222R	223L
P^2	ap					
	tr					
P^3	ap	23.85				
	tr	19.13				
P^4	ap					19.97
	tr					22.31
M^1	ap					
	tr			16.99	16.7	
M^2	ap	28.69		30.93		
	tr			24.27		
M^3	ap	49.71				49.99
	tr	29.62				33.69
dP^3	ap					
	tr		12.78	12.34		
dP^4	ap		19.62	15.82		
	tr		14.47	18.01		

		239L	239R	244L	244R	260
I^1	ap		18.8			
	tr		11.6			
I^2	ap		17.8			
	tr		8.4			
I^3	md					
C/	ap	25.8	22.2			
	tr	16.4	17			
P^1	ap					
	tr					
P^2	ap	12	7.3	12.36		
	tr	7.1	7	7.65		
P^3	ap	20.5	21.9			
	tr	19.4	18.9			
P^4	ap	18.8	17.7	19.31	20.24	
	tr	21.6	20.6	24.49	25.93	
M^1	ap	18e	20e	20	22.52	
	tr			20.9	20.84	
M^2	ap	26.7	24	32.01	30.64	27.9
	tr	25.3	25	24.68	25.6	20.4
M^3	ap	46.6	47.6			
	tr	34	33.6			

		264L	18566L	30159R	30162R
P^2	ap				10.03
	tr				6.5
P^3	ap				21.89
	tr		19.17		18.48
P^4	ap		20.22	18.3	17.47
	tr		23.45	22.5	21.7
M^1	ap		17.98	18.3e	
	tr			19.5e	
M^2	ap		28.51		
	tr		28.51		
M^3	ap	50.72			
	tr	31.24e			

Table 25 Continued

		30177	30177L	30177R	30268L	30268L
C/	ap	26.5				
	tr	15.4				
P^1	ap					
	tr					
P^2	ap					
	tr					
P^3	ap		22.27	22.54		
	tr		21.53	22.56		
P^4	ap		18.51	18.91		
	tr		21.96	23.2		
M^1	ap			21.08		
	tr			17.62		
M^2	ap					
	tr					
M^3	ap				51.89	51.5e
	tr					

		30268R	30413	30433L	30433R	30453R
P^2	ap			12.1		
	tr			7.9		
P^3	ap			22	22.3	23.7
	tr			21.5	20.7	
P^4	ap			19	18.4	18.7
	tr			23.7	24.3	23.2
M^1	ap		21.8	15.7e	15.7e	
	tr		19.9	20.7	18.4e	
M^2	ap			26e	27.4	
	tr			24	27.7	
M^3	ap	47.69				
	tr			31.4		28.9

		30474	30615	32515	30474R
P^3	ap	22.1	19.9		
	tr		16.3		
P^4	ap				
	tr	22.7			
M^1	ap				
	tr				
M^2	ap	24.9			25.43
	tr	24.8			24.91
M^3	ap	48.4		48.2	49.07
	tr			31.4	

Notochoerus cf. *Not. euilus*

(Figure 21; Tables 24, 29)

KANAPOI MATERIAL. 30184, female mand with symphysis (Rt. P_4–M_3, roots Lt. and Rt. I_1, /C).

One mandible, female from the size of its canines, has a third molar that terminates in a complex of pillars rather than in a fourth pair of pillars, thereby resembling the third molar of *Not. euilus*. The incisors and premolars are small but not as reduced as those of *Not. euilus* from the Lokochot Member at Koobi Fora (Harris, 1983b). At Lothagam, *Notochoerus euilis* is the predominant suid

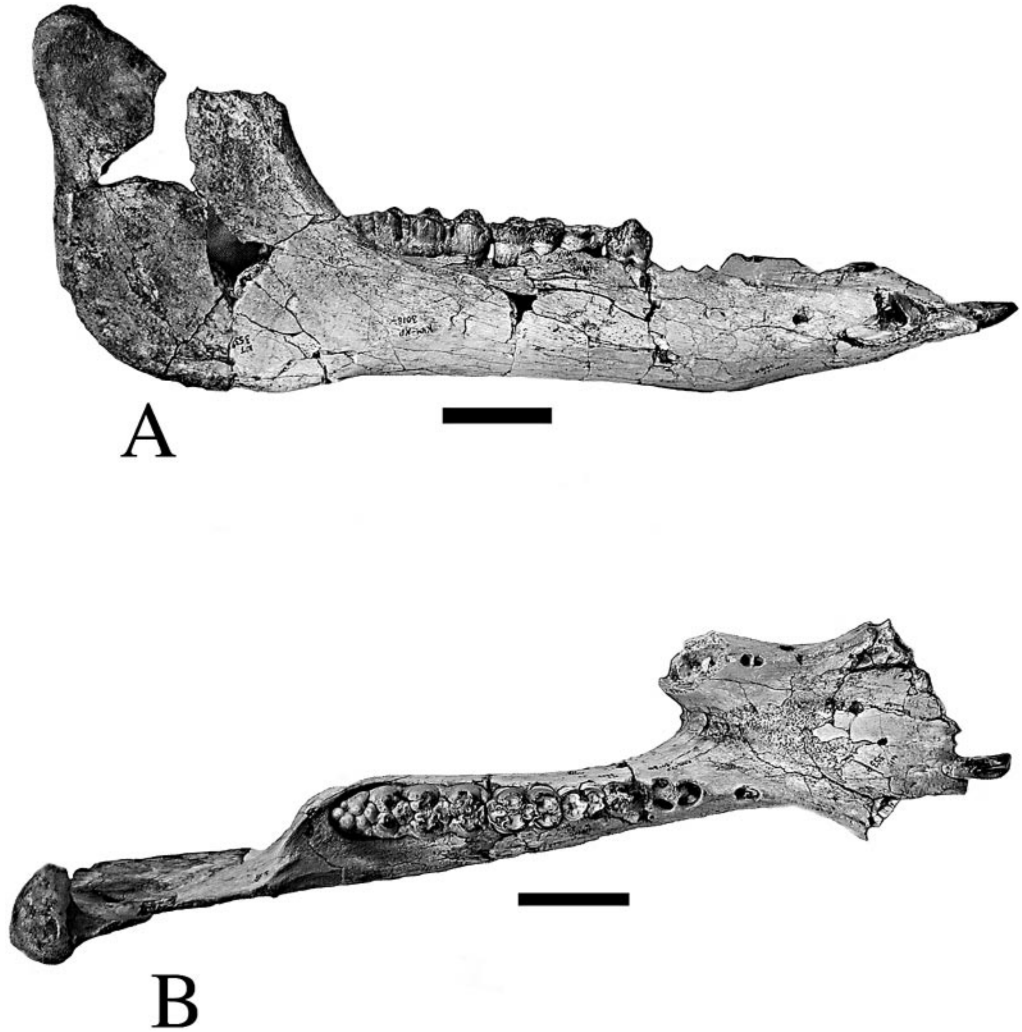

Figure 21 KNM-KP 30184, *Notochoerus* cf. *N. euilus* mandible; **A** = right lateral view; **B** = occlusal view; scales = 5 cm

in the Kaiyumung Member but there is a canine from the Apak Member that may also belong to that species.

Family Giraffidae

Giraffoids are rare elements of middle Miocene faunas in East Africa, being best represented by *Climacoceras africanus* MacInnes, 1936, at Maboko, *Climacoceras gentryi* Hamilton, 1978, at Fort Ternan, and *Palaeotragus primaevus* Churcher, 1970, from Fort Ternan and Ngorora (Hamilton, 1978). *Palaeotragus germaini*, first described from late Miocene localities in North Africa (Arambourg, 1959), has been reported from Lothagam (Churcher, 1979), as has a second smaller *Palaeotragus*, species (Harris, 2003a). Palaeotragines are not found at African Pliocene localities, their place being taken by more derived sivatheriines (*Sivatherium* Falconer and Cautley, 1832) and giraffines (*Giraffa* Brunnich, 1771), both probably being derived from Eurasia immigrant stock (Harris, 2003a).

Giraffa Brunnich, 1771

Giraffa stillei (Dietrich, 1942)

(Table 30)

KANAPOI MATERIAL. 30151, Rt. $M^{2\text{ or }3}$; 30428, Rt. P^4 and M_1; 30635, Lt. P_2; 30636, Rt. $M_{1\text{ or }2}$; 30637, upper tooth frags.

Giraffa stillei is a small species of *Giraffa* with teeth that are often smaller than those of *G. camelopardalis* (Linnaeus, 1798) and *G. jumae* Leakey, 1965, but always larger than those of *G. pyg-*

Table 26 Kanapoi *Nyanzachoerus pattersoni* lower teeth measurements

		202R	213L	215	219R	220R
P_2	ap					10.87
	tr					7.55
P_3	ap			24.56		28.31
	tr			19.47		22.28
P_4	ap			21.78	22.11	24.48
	tr			19.5		22.75
M_1	ap					
	tr					
M_2	ap			27.79	28.68	28.85
	tr			21.69	22.78	
M_3	ap		52.88	49.77		56.61
	tr	24.04	25.19	25.21		28.61

		221R	228	228L	236L	239L
I_1	ap					8.9
	tr					12
I_2	ap					12.3
	tr					14.6
I_3	ap					10.2
	tr					10
/C	ap					19.9
	tr					13.2
P_1	ap					
	tr					
P_2	ap					10.9
	tr					6.6
P_3	ap			27.52		
	tr			24.46		16.8e
P_4	ap			26.38		
	tr				20.45	
M_1	ap	21.79	19			
	tr	13.62	13.9			
M_2	ap			32.16	31.41	23.7
	tr			25.99		
M_3	ap					52.8
	tr					23

		239R	240L	240R	255L	256R	258L
I_1	ap	8.7					
	tr	11.7					
I_2	ap	10.9					
	tr	13.4					
I_3	ap	10.6					
	tr	8.7					
/C	ap	21.5					
	tr	13.4					
P_1	ap						
	tr						
P_2	ap	11					
	tr	6.7					
P_3	ap	22.8					22.74
	tr	17					19.88
P_4	ap						
	tr						
M_1	ap						
	tr						
M_2	ap		27.27	26.46	26.73		27.41
	tr		19.81	20.45	20.8		21.11
M_3	ap	53.3		54.62		53.87	60.17
	tr	22.9		24.05		23.78+	25.32

Table 26 Continued

		259L	260R	260R	262L	263L	264L
P_2	ap						11.26
	tr						7.78
P_3	ap			23.26			26.62
	tr			19.78			20.69
P_4	ap			20.61			23.71
	tr			19.4			21.58
M_1	ap		19.87	19.21		19.5	
	tr		13.64	14.5		13.18	
M_2	ap			25.98	33.73	26.19	27.64
	tr			20.14	25.8	18.06	
M_3	ap	54.21		48.79			56.32
	tr			22.53			28.86

		266L	533R	534L	30160	30161	
I_1	ap				13.4		
	tr				15.6		
I_2	ap				12.4		
	tr				17.4		
I_3	ap						
	tr						
/C	ap				22.8		
	tr				15.3		
P_1	ap						
	tr						
P_2	ap				8.2		
	tr				7.5		
P_3	ap				27.3	24.7	
	tr				20.9	17.5	
P_4	ap				24.4		
	tr				21.3		
M_1	ap						
	tr						
M_2	ap	24.64			26.4		
	tr	19.39			22.7e		
M_3	ap			56.48	50.6	49.2	
	tr		25.6	26.72	26.4	25.6	

		30161R	30168R	30177L	30177R	30177R	30179L
I_1	ap					13.4e	
	tr					10.9	
I_2	ap					14.7	
	tr					13.8	
I_3	ap					8.6	
	tr					12.5	
/C	ap						
	tr						
P_1	ap						
	tr						
P_2	ap			9.08	9.85		
	tr			8.25	7.78		
P_3	ap		24.4	25.23	25.71		
	tr		17.5	21.36	19.51		
P_4	ap	20.7					
	tr	16.3					
M_1	ap						
	tr						
M_2	ap	24.3					
	tr	19.7					
M_3	ap	52.9e	48.43				75.67e
	tr	24.1	25.65				

Table 26 Continued

		30183L	30205R	30267L	30267R	30267L
I_1	ap		9.1			
	tr		12e			
I_2	ap		12e			
	tr		13.6e			
P_2	ap	9.97	8.7			
	tr	7.81	7.42			
P_3	ap	25.61	27.45	24.84	23.56	25.3
	tr	19.75	21.03	18.27	18.31	18.2
P_4	ap	22.47	22.5	21.78	21.22	22
	tr	20.34	21.33	18.51	20.06	20
M_1	ap				17.83	18
	tr					
M_2	ap		26.09		28.1	28.5
	tr		23.52E		21.31	21.5
M_3	ap	54.34	52.16		54.06	54.8
	tr	24.23	27.64		25.26	24.9

		30267R	30403	30409	30410L	30410R	30456
/C	ap	32.3					
	tr	22.9					
P_1	ap						
	tr						
P_2	ap	10					
	tr	7.1					
P_3	ap	25.3			25.0	25.5	
	tr	18.5			17.5	18.7	
P_4	ap	22.2		23	23.5	22.0	
	tr	19.5		19	20.9e	20.5	
M_1	ap	19.2			20.8e		
	tr	15.5					
M_2	ap	28.5		26			26
	tr	22		19.2			17.1
M_3	ap	54.5	50.7e	50e		55.6e	
	tr	24e	23.3	22.6			

		30458L	30458	30462	30475	30475L	30545
I_3	ap						10.1
	tr						8.5
/C	ap						
	tr						
P_1	ap						
	tr						
P_2	ap	10.32					
	tr	7.12					
P_3	ap	22.91			26.6		
	tr	18.29			24.4		
P_4	ap	21.45			26.2e		
	tr	19.64					
M_1	ap	18.06					
	tr	14.88					
M_2	ap	27.4	28.9	29	33	30.24	
	tr	21.26	20.8	21.5e	26	19.87	
M_3	ap	54.43					
	tr	23.94					

Table 26 Continued

		30620	32539	32553
I_3	ap			13.7
	tr			15.5
/C	ap			
	tr			
P_1	ap			
	tr			
P_2	ap			
	tr			
P_3	ap			
	tr			
P_4	ap	23.2	21.2	
	tr	20.3	19.1	
M_1	ap	19.5	18.1	
	tr	15.6	14.6e	
M_2	ap	27.4	25	
	tr	21.8	19.7	
M_3	ap	58.7e	50	
	tr		24.3	

maea Harris, 1976. The ossicones are uprightly inserted like those of *G. camelopardalis* but appreciably smaller than male specimens of the extant species and often lack well-developed terminal knobs; they are larger than specimens assigned to *G. pygmaea* but are not backwardly raked like those of *G. jumae*.

Five isolated teeth attributed to *G. stillei* are smaller than those of extant giraffes except for one anterior lower premolar (KP 30365) that is about the same size as that of the extant species.

Giraffa jumae Leakey, 1965

(Table 31)

KANAPOI MATERIAL. 30450, Lt. mandible (P_2–M_3).

Giraffa jumae is a large species of giraffe of similar size to the extant *G. camelopardalis*. The surface of the frontal bone between the external rims of the orbits is nearly flat. The width of the skull roof between the orbits is greater than in *G. camelopardalis*. The longitudinal median section from the posterior edge of the nasals to the lateral ossicone is flat or slightly concave. The lateral ossicones originate immediately above the orbit and project more posteriorly than in *G. camelopardalis*. No secondary bone apposition is known to occur on the lateral ossicones. The median ossicone is poorly developed. The basilar process of the occipital is longer than the external width of the palatal area at M^2. The ascending ramus of the mandible is wide and stout. The corpus is deep and long, the anterior portion of the corpus being inclined upward from the premolars to the symphysis and then downward in the incisive region.

Only one mandible of *G. jumae* has been recovered from Kanapoi. The lower teeth are somewhat larger than those of extant giraffes and the anterior premolar (P_2) is significantly larger.

Giraffa sp. indet.

(Table 32)

KANAPOI MATERIAL. 98, distal metacarpal; 480, prox phalanx; 472, Lt. astragalus; 473, Rt. astragalus frag; 30446, prox metacarpal; 42091, Lt. radioulna; 42092, Lt. radioulna, Lt. metacarpal, Lt. cuneiform, Lt. semilunar; 42093, Lt. tibia and Rt. humerus.

None of the postcranials were found in association with teeth or ossicones. All are somewhat smaller than those of extant giraffes and thus are more likely to represent *Giraffa stillei* rather than *G. jumae*.

Sivatherium Falconer and Cautley, 1832

Sivatherium hendeyi Harris, 1976

Sivatherium hendeyi is of similar size and dental morphology as the Asian *S. giganteum* Falconer and Cautley, 1832, and the later African species *S. maurusium* Pomel, 1892, but the posterior ossicones are short, extending laterally and backward from the cranium, and are unornamented by knobs or flanges or palmate digitations. The metacarpals longer than in *S. giganteum* or in Pleistocene specimens of *S. maurusium* (after Harris, 1976b).

Sivatherium cf. *S. hendeyi*

(Table 33)

KANAPOI MATERIAL. 135, Lt. fibula; 30227, upper and lower molar frags; 30449, prox Rt. ossicone frag; 32551, Rt. M/ and Rt. M_3 frags.

The proximal right ossicone fragment is trian-

Table 27 Kanapoi *Notochoerus jaegeri* upper teeth

		211L	225L	225R	234L
P^2	ap		11.48	11.37	
	tr		7.15	7.42	
P^3	ap	23.01	22.49	21.12	
	tr	20.03E	19.07	19.43	
P^4	ap	15.86	19.05	18.38	
	tr	19.21	21.83	21.89	
M^1	ap				
	tr				
M^2	ap		25.56	23.95	
	tr		26.39	24.36	
M^3	ap		47.22	49.37	66.89e
	tr		33.45	33.68	32.59e
dP^3	ap				
	tr				
dP^4	ap				
	tr				

		253R	257L	257R	26944	26944L
P^2	ap					
	tr					
P^3	ap		21.83	24.15		
	tr		19.42	18.39		
P^4	ap		18.76	16.39		
	tr		20.98	21.37		
M^1	ap					
	tr					
M^2	ap		30.86	29.79		
	tr		25.14	25.71		
M^3	ap	71.78	63.82	63.77	71.2	72.31
	tr	33.23	35.46	36	36.8	36.99

		30617L	30617R
P^2	ap		
	tr		
P^3	ap		23.0
	tr		21.0
P^4	ap	22.3e	
	tr	20.8	
M^1	ap		
	tr		
M^2	ap	35.8	
	tr	25.9	27e
M^3	ap	74.0	74.2
	tr	35e	36.9

gular in transverse section with convex anteromedial and anterolateral surfaces and a flattened posterior surface. The ossicone has a basal sinus and is massive proximally but tapers above the base. The ossicone is somewhat bovine in appearance and appears to have extended outward and backward at the base but curves medially. The anterior surfaces are marked with deep longitudinal grooves. Compared with ossicones of *S. maurusium,* this specimen is smaller, more gracile, and lacks the lateral bosses. Compared with the horn cores of the bovin *Simatherium* Dietrich, 1941, the ossicone lacks the strong dorso-ventral compression of the bovin horn core and tapers less gradually distally.

The giraffid tooth fragments assigned to *Sivatherium* are much larger than the teeth in the *G. jumae* mandible.

Harris (1976b) proposed the name *S. hendeyi* for the Langebaanweg sivatheres, which were characterized by ossicones that were shorter and simpler than those of *S. maurusium* from younger sites. Churcher (1978) did not use this name but thought the Langebaanweg sivatheres may represent an ancestral African sivathere population. We now know that Pliocene sivathere metapodials associated with *S. maurusium* ossicones were originally of similar length to those of *S. hendeyi* but underwent a dramatic reduction in length when *S. maurusium* adopted a grazing diet at the end of the Pliocene (Harris and Cerling, 1998; Cerling et al., in press). The Kanapoi ossicone is referred to *S. hendeyi* on the basis of its size and morphology.

Family Bovidae

The family Bovidae is sparsely represented at early Miocene localities in East and North Africa (Hamilton, 1973; Gentry, 1978) but bovids were the most numerous terrestrial mammals at the mid-Miocene site of Fort Ternan (Gentry, 1970) and they dominate younger vertebrate fossil assemblages from eastern Africa. Bovids occur in both Eurasia and Africa during the early Miocene, and thereafter, migrations occurred between them repeatedly (Vrba, 1985, 1995) but Gentry (1990) argues for Africa as the origin of this family. Because the sole apomorphic character characterizing the family Bovidae is the presence of horn cores (Janis and Scott, 1987), it would be difficult to substantiate a hornless bovid ancestor with any degree of certainty.

The Antilopini and Caprini, both of Eurasian origin, are first represented in Africa about 14 million years ago; the endemic Cephalophini and Neotragini make their appearance shortly thereafter. Toward the end of the Miocene, Ovibovini and Bovini migrated into Africa from Eurasia while the endemic Tragelaphini, Hippotragini, Alcelaphini, and Aepycerotini are documented for the first time. The Reduncini, whose continent of origin is uncertain, also appear in the late Miocene whereas the Boselaphini become extinct in Africa near the Mio–Pliocene boundary (Vrba, 1985).

The Kanapoi bovid assemblage is dominated by tragelaphins, alcelaphins, and aepycerotins—suggesting a mixture of open and closed mesic to xeric habitats. Boselaphins, common elements in the Nawata Formation at Lothagam and persisting into the Apak Member (Harris, 2003b), have yet to be recovered from Kanapoi.

Table 28 Kanapoi *Notochoerus jaegeri* lower teeth measurements

		210R	226	235R	235L
P_2	ap				
	tr				
P_3	ap				
	tr		13.4		
P_4	ap			21	
	tr				
M_1	ap				
	tr				
M_2	ap				
	tr				
M_3	ap	80.56			67.66
	tr	27.89			27.06

		241R	267R	251L	251R	252R
P_2	ap					
	tr					
P_3	ap	23.86	22.55	23.97	22.48	
	tr	16.71	13.74	16.84	16.78	
P_4	ap		18.1	19.89		
	tr		15.32	17.18		
M_1	ap					20.44
	tr					13.81
M_2	ap					
	tr					
M_3	ap			64.55	61.18	
	tr			25	25.07	

		267L	269R	30178L	30178R
P_2	ap				
	tr				
P_3	ap			25.85	25.55
	tr			17.92	17
P_4	ap			20.88	
	tr			18.48	17.8e
M_1	ap		26.6		
	tr		14.05		
M_2	ap			34.06	35.79
	tr			23.55	24.65e
M_3	ap	81.97		77.28	80.87
	tr	28.37		30.34	30.37

		30180L	30182L	30402	30550	32258
P_2	ap					
	tr					
P_3	ap	23.6				
	tr	16.4				
P_4	ap	19.7				
	tr	17.1				
M_1	ap					
	tr	16				
M_2	ap	31	32			35.6
	tr	22e	20.2+	22.3		23.6
M_3	ap	70.2		76.6	82	78.9
	tr	24.9		30.3	29+	29.6

Table 28 Continued

		32801	30180L	30182R	30452R	30452L
P_2	ap					
	tr					
P_3	ap	23.62		26.61		26.48
	tr	16.49		17.64		
P_4	ap	19.47		20.68		20.46
	tr	17.11				
M_1	ap	19.4				
	tr	15				
M_2	ap		31.78	35.51		29.18
	tr			19.95	21.22	
M_3	ap	76e	71.99		71.65	71.51
	tr	26e	25.04		23.8	24.7e

Tribe Tragelaphini

Tragelaphus Blainville, 1816

Tragelaphus species are medium to large tragelaphins with spiraled horn cores inserted close together and having an anterior keel and sometimes a stronger posterolateral one; small- to medium-sized supraorbital pits, which are frequently long and narrow, and an occipital surface tending to have a flat top edge and straight sides (Gentry, 1985). The genus *Tragelaphus* is diverse, including the kudus, the nyalas, the sitatunga, and the more ubiquitous bushbuck. Greater and lesser kudus occur today in the northern half of the Turkana Basin.

Tragelaphus kyaloae Harris, 1991

(Table 34)

KANAPOI MATERIAL. 68, occiput; 77, Lt. h/c frags; 78, Lt. h/c frag; 79, Rt. and Lt. h/c frags; 80, Lt. h/c frag; 81, Rt. h/c frags; 82, Rt. h/c frags; 84, dist Rt. h/c frag; 86, Lt. h/c frags; 87, dist Lt. h/c; 88, dist. Rt. h/c frag; 89, dist. Rt. h/c frag; 90, prox

Table 29 Kanapoi *Notochoerus euilus* lower tooth measurements

		30184R
I_2	md	11.7
	bl	13.6
P_2	ap	
	tr	
P_3	ap	
	tr	
P_4	ap	20.5
	tr	16.7
M_1	ap	21.0
	tr	14.9
M_2	ap	32.4
	tr	21.4
M_3	ap	73.5
	tr	25.8

Table 30 Kanapoi *Giraffa stillei* tooth measurements

		KP 30635	KP 30636	KP 30637A	KP 30637B	KP 30428	30151
P/	ap					18.51	
	tr					16.43	
M/	ap				25.37	21.22+	23.16
	prot			25.41			24.45
	met						21.65
P_2	ap	15.25					
	tr	10.61					
P_3	ap						
	tr						
P_4	ap						
	tr						
M_1	ap		23.74				
	prot		16.47				
	met		16.64				
M_2	ap						
	prot						
	met						
M_3	ap						
	prot						
	met						

Rt. h/c frag; 91, prox Lt. h/c frag; 92, frontlet and prox Rt. h/c; 29258, prox Rt. h/c frag; 29260, prox Rt. h/c; 29261, prox Rt. h/c; 29268, prox Rt. h/c; 29269, dist Rt. h/c; 29272, prox Lt. h/c; 29278, dist Rt. h/c; 30156, h/cs and frontlet; 30158, calvaria and h/cs; 30445, prox Rt. h/c; 30448, h/c frags; 30486, dist. Rt. h/c; 30628, dist Lt. h/c frag; 30629, Rt. h/c frag; 30634, prox Lt. h/c; 32519, prox Rt. h/c frag; 32559, dist. Rt. h/c frag; 29266, dist Lt. h/c.

Tragelaphus kyaloae is a medium-sized tragelaphin with horn cores inserted close together, at a low inclination, that diverge rapidly from their base but converge distally, and that spiral 180° anticlockwise in the right horn core. Proximally, there is a strong posterolateral keel and a fainter anterolateral keel; distally, these become anterolateral and posteromedial, respectively. The shape of the horn cores is reminiscent of the extant sitatunga (*T. spekei* Sclater, 1863); they are less helically coiled than in *T. strepsiceros* (Pallas, 1766), *T. imberbis* Blyth, 1869, or *T. gaudreyi* (Thomas, 1884) but converge closer distally than in *T. nakuae* Arambourg, 1941, or the kudu-like species. The cranial vault bears a faint but distinct transverse bar immediately in front of the nuchal crest. The paroccipital processes are short but stout, and the posterior tuberosities of the basioccipital are much wider than the anterior ones.

Table 31 Kanapoi *Giraffa jumae* tooth measurements

		KP 30450
P_2	ap	20.62
	tr	13.62+
P_3	ap	25.03
	tr	19.83
P_4	ap	26.15
	tr	22.17
M_1	ap	28.81
	prot	
	met	
M_2	ap	29.76
	prot	22.52
	met	22.62
M_3	ap	46.42
	prot	23.89
	met	21.56

This is by far the most abundant bovid in the Kanapoi biota. The holotype of *T. kyaloae* is from the lower Lokochot Member at Kosia (Harris, 1991b) and it is the common tragelaphin in the Lokochot and Moiti Members of the Koobi Fora Formation (Harris, 2003b). The oldest documented occurrence of this taxon is a single specimen from the Upper Nawata at Lothagam but it is also represented by a dozen horn cores from the Apak and Kaiyumung Members of the Nachukui Formation at Lothagam. The horn cores are similar in cross-section to those of *T. nakuae*, the common Pliocene tragelaphin of the Lake Turkana Basin, but have more pronounced torsion.

Tragelaphini gen. indet.

(Table 35)

KANAPOI MATERIAL. 32514, Lt. maxilla (P^4–M^3); 66, Rt. mandible ($M_{2–3}$); 67, Lt. mandible frag (M_1); 76, Lt. M^1; 109, Lt. M^1; 29273, Lt. and Rt.

Table 32 Kanapoi *Giraffa* sp. indet. postcranial measurements

	Specimen	Length	Prox ap	Prox tr	Dist ap	Dist tr	Epic tr
42093	Humerus				119.5	110.42	125.58
42092	Radius		70.43	115.14	66.48	106.77	
42092	Prox ulna			63.31			
98	Metacarpal				61.8	92.15	
30446	Metacarpal		37.43	65.01			
42092	Metacarpal		66.7	97.7	57.63	86.53	
42093	Tibia				76.59	102.95	
480	Proximal phalanx	66.98	33.2	33.15	22.48	27.86	

		Max ap	Max tr	Max dv
42092	Cuneiform	69.5	35.0	60.5
42092	Semilunar	61.4	43.5	48.0

M$^{1-2}$; 30395, Lt. M$^{1-2}$; 30396, Lt. M^3; 30421, Rt. M$_1$, Lt. M$_2$, Rt. M$_3$; 30441, Lt. M^1; 32545, Lt. mandible frags (P$_2$–M$_1$); 32570, Lt. mandible frags, P$_3$–M$_1$; 32573, M/, Lt. M$_1$, and tooth frags; 32574, Lt. M$_1$; 32829, upper and lower molar frags; 32881, Rt. P$_3$; 36861, Rt. mandible (P$_{3-4}$) and bone frags.

A number of isolated tragelaphin dentitions were recovered. Most are of similar size and presumably represent *Tragelaphus kyaloae* but the smaller KP 32514 indicates that at least two tragelaphin species were present at Kanapoi.

Tribe Bovini

Simatherium Dietrich, 1941

Only one extant bovin species, *Syncerus caffer* (Sparrman, 1779), is endemic to sub-Saharan Africa but three other genera—*Ugandax* Cooke & Corydon, 1970, *Simatherium,* and *Pelorovis* Reck, 1928—are represented in the fossil record. *Simatherium* differs from *Ugandax* by being larger and having more widely separated horn cores that are more divergent basally and more curved anteriorly. The more derived *Pelorovis*, is unknown before the late Pliocene. *Simatherium kohllarseni* Dietrich 1942 was originally described from Laetoli in Tanzania whereas the somewhat older *Simatherium demissum* Gentry, 1980, was first described from Langebaanweg in South Africa.

Simatherium demissum Gentry, 1980

Simatherium cf. *S. demissum*

(Figures 22, 23; Tables 36, 37)

KANAPOI MATERIAL. 96, Rt. mandible (P$_2$–M$_3$) and assoc postcranial; 29265, skull frags, Lt. maxilla (P^2–M^3), Rt. maxilla (P^4, M$^{2-3}$); 30612, broken skull with Rt. and Lt. h/cs; 32560, Lt. M^1 frag.

Table 33 Kanapoi *Sivatherium* fibula measurements

	Length	Prox tr	Dv
135	55.79	31.42	33.85

This Kanapoi bovin is represented by a very battered calvaria with portions of both horn cores and by a partial upper dentition, both collected by National Museums of Kenya parties, and by a mandible and associated postcranial elements that were collected by the Harvard University expedition. The horn cores are strongly dorso-ventrally compressed. They extend outward and backward from their bases but ascend upward toward their tips. The horn cores taper gently in their proximal portion but more rapidly toward their tip. The surface of the horn cores is not well enough preserved to confirm the presence or absence of a lateral keel but are otherwise ornamented by strong longitudinal ridges and furrows. Although the bone is very incompletely preserved, the braincase evidently extended for some distance behind the horn cores and was bordered by well-developed temporal fossae. There was a strong interfrontal crest.

Tribe Hippotragini

There are three extant genera of hippotragins—*Hippotragus* Sundevall, 1846 (roan and sable antelopes), *Oryx* Blainville, 1816, and *Addax* Rafinesque, 1815, and several extinct genera. Vrba (1987) suggested that, early in their history, the hippotragins diverged into two major subclades—one exemplified by *Hippotragus,* with uprightly inserted and mediolaterally compressed horn cores, and the other by the less water-dependent *Oryx* and *Addax,* with horn cores that are less mediolaterally compressed but bent more strongly backwards.

Hippotragini gen. indet.

(Figure 24; Table 38)

KANAPOI MATERIAL. 483, B–D, Lt. P^4–M^1, Lt. M^3, Rt. M^2; 29274, Rt. mandible (M$_{2-3}$); 30631, proximal Rt. h/c; 32526, Lt. M^1.

This taxon is represented by the proximal portion of a large right horn core that is mediolaterally

Figure 22 KNM-KP 30612, *Simatherium* cf. *S. demissum*, calvaria, dorsal view; scale = 5 cm

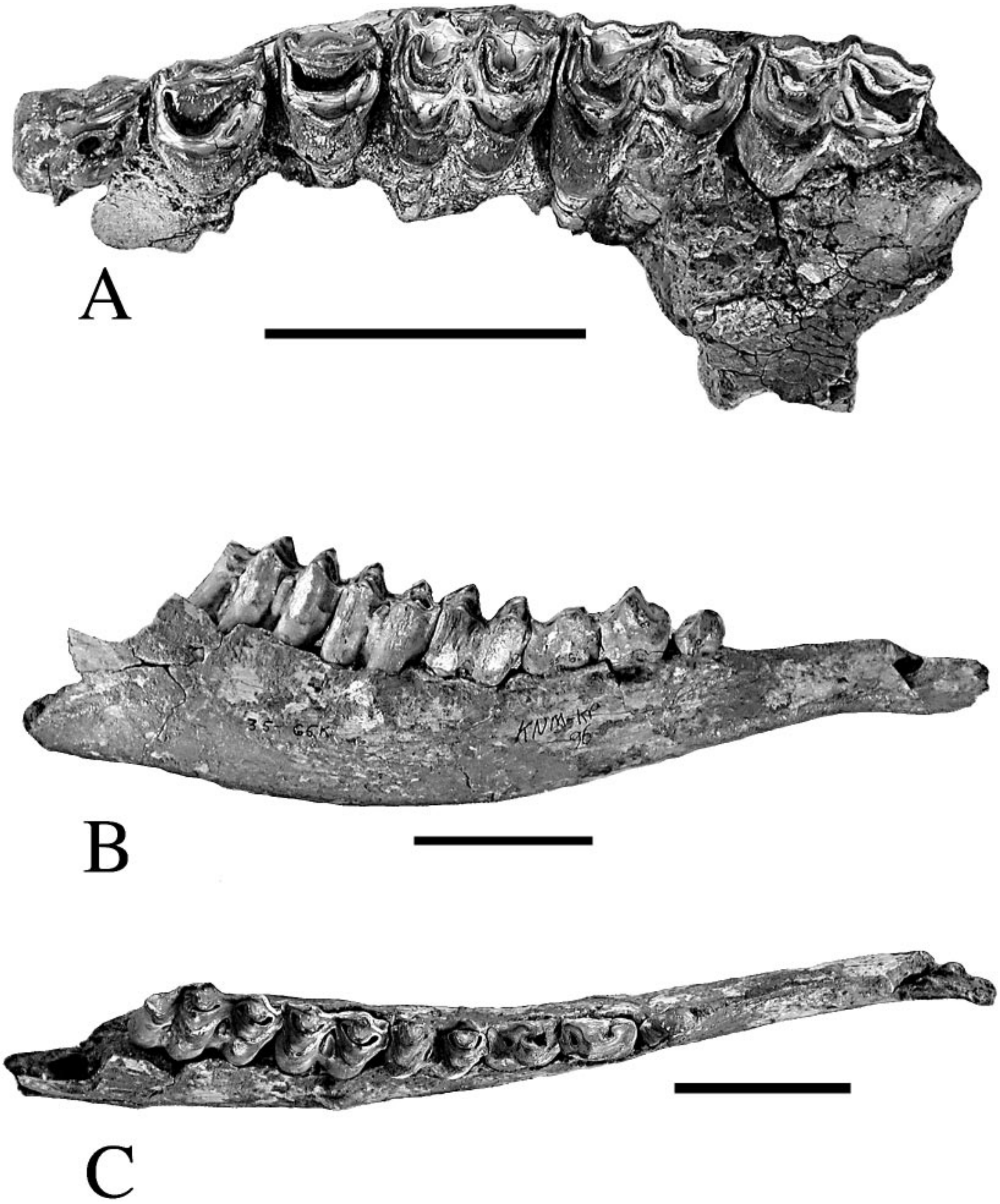

Figure 23 *Simatherium* cf. *S. demissum*, dentitions; **A** = KNM-KP 29265, left maxilla, dorsal view; **B** = KNM-KP 96, right mandible (P_3–M_3), lateral view; **C** = KNM-KP 96, occlusal view; scales = 5 cm

compressed with a flattened lateral surface. The horn core curves gently backward from its base with a slight lyrate flexure in anterior view. There is faint transverse annulation on the anterior surface. At its base, the horn core measures 46.1 mm anteroposteriorly; the transverse measurement is 33.9 mm.

A few hippotragin teeth were recovered although none were associated with the sole recognized hippotragin horn core.

Tribe Reduncini

Reduncins are small to large antelopes with hypsodont teeth for grazing and today characteristically occur in grasslands near permanent water. There are two extant genera—*Kobus* Smith, 1840 (water-

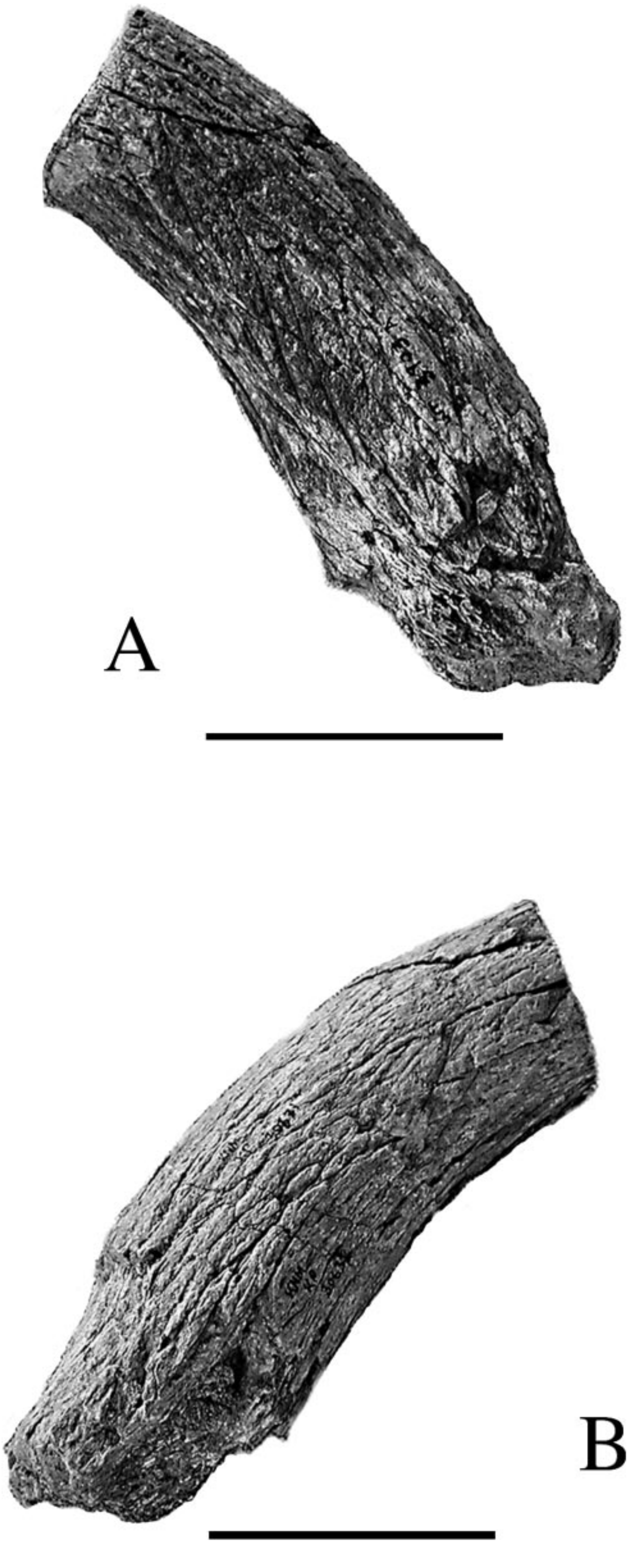

Figure 24 KNM-KP 30361, Hippotragini gen. indet., proximal right horn core; **A** = lateral view; **B** = medial view; scales = 5 cm

Table 34 Kanapoi *Tragelaphus kyaloae* horn core measurements

	prox ap (Rt)	prox tr (Rt)	lt (Rt)	prox ap (Lt)	prox tr (Lt)	lt (Lt)
77				38	53.12+	
78				38	50	
79	41	50				
80				33	44	
81	31+					
86				33	47	
90	37	45				
91				43	56	
92	38	46				
29258	38	49				
29260	40	53				
29261	37	48				
29268				39	51	
29272				38	46	
30156	38	50		38	49	
30158	42	54		41	55	
30445	38	53				
30634	34	52				

bucks, kobs, etc.) and *Redunca* Smith, 1827 (reedbucks). The earliest recognized species of *Kobus* are from Lukeino and Lothagam.

Kobus Smith, 1840

Kobus sp. indet.

KANAPOI MATERIAL. 461, Rt. h/c frags; 29267, proximal Rt. h/c.

KP 29267 is a small but stout horn core that curves backward and slightly outward from its base. The horn core tapers gently upward from its base and the lateral surface is slightly flattened. At its base, KP 29267 measures 35.5 mm anteroposteriorly and 28.2 mm transversely. Corresponding measurements for KP 461 are 34.9 and 28.8 mm. The two horn cores are smaller than those of *K. presigmoidalis* Harris, 2003b, from Lothagam.

Reduncini gen. indet.

(Table 39)

KANAPOI MATERIAL. 75, Rt. P_3; 463, Lt. mandible (M_1); 29275, Rt. maxilla (P^4–M^3); 29276, Rt. mandible (P_2–M_1); 29279, Rt. mandible (P_2, M_{1-3}); 30626, Lt. mandible (P_4–M_1); 27450, Lt. M_1.

A few reduncin teeth were recovered but none were associated with the *Kobus* horn core.

Tribe Alcelaphini

Alcelaphins are represented by four extant genera: *Damaliscus* Sclater and Thomas, 1894, *Beatragus* Heller, 1912, *Alcelaphus* de Blainville, 1816, and *Connochaetes* Lichtenstein, 1814, plus a number of extinct genera. All the extant genera are specialist bulk grazers that are capable of going without water for varying intervals of time. *Damalacra* species were originally described from Langebaanweg (Gentry, 1980) and the genus was subsequently recognized at Lothagam (Harris, 2003b) and elsewhere. A cladistic analysis of fossil and living Alcelaphini by Vrba (1997) suggested that two alcelaphin subtribes diverged during or before the Mio–Pliocene transition—the Alcelaphina (*Damalacra neanica* Gentry, 1980, and *Beatragus*) and the large clade Damalascina (which includes the *Damaliscus* and *Parmularius* Hopwood, 1934 lineages). Both subtribes appear to be represented at Kanapoi.

Damalacra Gentry, 1980

Damalacra neanica Gentry, 1980

Horn cores of *Damalacra neanica* are without compression or are slightly compressed anteroposteriorly, have no flattened lateral surface, taper fairly sharply from base to tip, show much increased divergence distally, have either slight forward or slight backward curvature in profile, and are inserted behind or above the back of the orbits. The boundary between the pedicel top and the base of the horn core is higher on the medial than on the lateral side of the horn cores. Female horn cores are smaller than those of males, as in extant alcelaphins (after Gentry, 1980).

Damalacra cf. *D. neanica*

(Figure 25)

KANAPOI MATERIAL. 71, frontlet with Rt. and Lt. h/cs.

The sole specimen comprises a frontlet with proximal horn cores that have long pedicels hollowed out by very large basal sinuses. The horn cores diverge outward and taper rapidly upward from their bases. They are ornamented by strong longitudinal ridges and furrows. The face was evi-

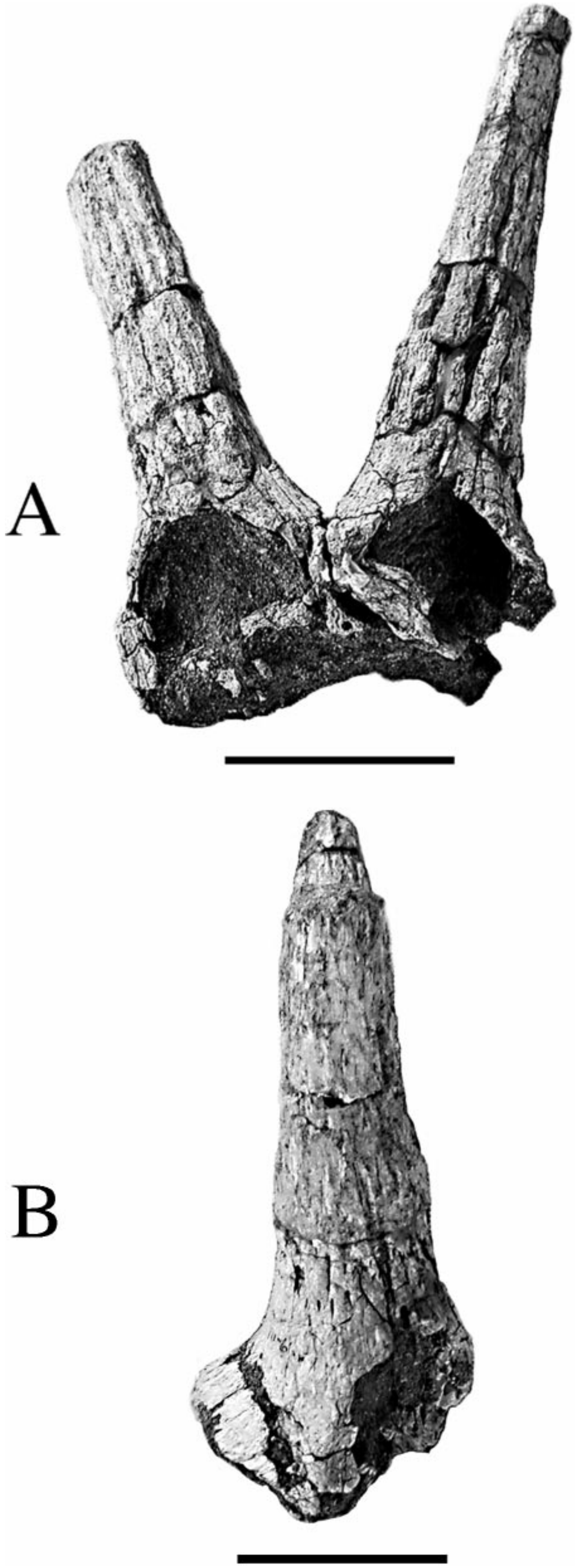

Figure 25 KNM-KP 71, *Damalacra* cf. *D. neanica* frontlet with proximal horn cores; **A** = anterior view; **B** = right lateral view; scales = 5 cm

Table 35 Kanapoi Tragelaphini dentition measurements

		109	29273L	29273R	30395	32514
P^4	ap					10.3
	tr					14.4
M^1	ap	23.0	21.2	21.5	18.9	13.8
	tr	16.9	15.9	15.4	23.0	14.2
M^2	ap		21.8	22.8	27.8	18.1
	tr		16.6	17.0	24.0	17.8
M^3	ap					21.7
	tr					16.2

		30396	30441
M^1	ap		19.7
	tr		16.5
M^2	ap		
	tr		
M^3	ap	26.1	
	tr	14.4	

		66	67	32574	32881	32570
P_3	ap				11.9	12.9
	tr				7.4	8.0
P_4	ap					14.4
	tr					8.9
M_1	ap			17.6		15.9
	tr			10.2		10.8
M_2	ap	19.0	18.9			
	tr	13.0				
M_3	ap	29.9				
	tr	12.7				

		32545	32573	30421	36861
P_2	ap	10.2			
	tr	5.7			
P_3	ap				10.6
	tr				6.0
P_4	ap	16.5			11.0
	tr	8.3			5.8
M_1	ap			16.0	
	tr			10.4	
M_2	ap	20.9	18.9	20.0	
	tr	12.5	12.3	12.2	
M_3	ap			26.1	
	tr			12.0	

dently strongly angled on the braincase. From the width of the preserved portion of the braincase at the base of the horn cores, this was evidently a much larger animal than *Damalacra* species A or B from Lothagam (Harris, 2003b). The base of the right horn core measures 36 mm (anteroposteriorly) by 33 mm (transversely); the left horn core measures 24 × 33 mm.

This specimen is closer to *D. neanica* than to *D. acalla* Gentry, 1980, by virtue of the uncompressed and widely divergent horn cores, but the horn cores are smaller than male representatives of this species from Langebaanweg.

Table 36 Kanapoi *Simatherium* cf. *S. demissum* horn core measurements

		30612
Lt h/c	ap	86
	tr	65
Rt. h/c	ap	
	tr	
	lt	290+
Width between h/cs		160

Damalacra sp. A

(Figure 26; Table 40)

KANAPOI MATERIAL. 64, proximal Lt. h/c; 26560, proximal Lt. h/c; 29270, Rt. h/c; 30630, distal h/c frags; 30447, proximal Lt. h/c.

This species had a long, slender horn core very reminiscent of specimens attributed to *Damalacra* sp. A from Lothagam (Harris, 2003b). The horn core was mediolaterally compressed with a flattened lateral surface. It tapers gently upward from the base. It is teardrop-shaped in transverse section with a carinate posterior border. The horn cores diverge outward and slightly backward from the

Table 37 Kanapoi *Simatherium* cf. *S. demissum* teeth measurements

		29265L	29265R
P^2	ap	19.18	
	tr	17.47	
P^3	ap	18.52	
	tr	22.37	
P^4	ap	16.72	16.88
	tr	22.3	
M^1	ap	23.1	
	tr	24.73	
M^2	ap	27.86	27.03
	tr	27.43	
M^3	ap	29.98	30.36
	tr	25.77	29.43

		96
P_2	ap	14.64
	tr	9.31
P_3	ap	20.19
	tr	11.61
P_4	ap	21.66
	tr	13.24
M_1	ap	21.75
	tr	17.18
M_2	ap	27.97
	tr	17.71
M_3	ap	37.98
	tr	17.09

Figure 26 KNM-KP 29270, *Damalacra* sp. A, right horn core; **A** = lateral view; **B** = medial view; scale = 5 cm

Table 38 Kanapoi Hippotragini teeth measurements

		32526	483 B–D
P^4	ap		11.5
	tr		11.2
M^1	ap	21.1	19
	tr	23.8	13.7
M^2	ap		20.2
	tr		15.5
M^3	ap		25.1
	tr		15.9

		29274
M_2	ap	24.91
	tr	14.41
M_3	ap	30.93
	tr	14.1

base but recurve to upright in their distal portion. There are faint transverse annulations on the anterior surface and strong longitudinal ridges and furrows on the lateral and medial surfaces.

Damalacra acalla Gentry, 1980

The cranium of *Damalacra acalla* is of similar size and proportions to that of *D. neanica*. The horn cores are mediolaterally compressed with localized (usually medial) swelling at their bases, sometimes with flattened lateral surface along part of their length, with more definite backward curvature than in *D. neanica* and less marked distal divergence, inserted close behind orbits, and with a more nearly horizontal boundary between the top of the pedicel and the horn core proper. Other differences from *D. neanica* are that the braincase roof is less steeply inclined, more curved in profile, and with a parietal hump that is as well developed as in living *Damaliscus*; the mastoid exposure is large but less expanded especially medioventrally, and the auditory bullae are slightly larger and much more inflated. Female horn cores are smaller than those of the males. The teeth are of similar morphology to *D. neanica* (after Gentry, 1980).

Table 39 Kanapoi Reduncini tooth measurements

		29275
P^2	ap	
	tr	
P^3	ap	
	tr	
P^4	ap	
	tr	
M^1	ap	13.8
	tr	17.6
M^2	ap	18.1
	tr	21.8
M^3	ap	22.1
	tr	

		75	463	29275	29276	29279	30626
P_2	ap				8.0	7.7	
	tr				6.9	4.6	
P_3	ap	10.4			11.7		
	tr	6.9			9.0		
P_4	ap				14.9		14.1
	tr				9.2		7.8
M_1	ap		16.1	15.8	16.0	17.3	
	tr		9.6	10.7	11.8	13.0	
M_2	ap					19.6	
	tr					14.3	
M_3	ap					31.1	
	tr					14.8	

Table 40 Kanapoi *Damalacra* sp. A horn core measurements

		26560	64A	29270	30447
Rt h/c	ap			23.9	
	tr			17.6	
	lt			160+	
Lt h/c	ap	23.8	22.3		21.1
	tr	18.3	17.4		18.1
	lt				

Damalacra cf. *D. acalla*

(Figure 27; Table 41)

KANAPOI MATERIAL. 30157, calvaria with Rt. and Lt. h/cs; 32557, proximal Rt. h/c frag; 32876, distal h/c frag.

This alcelaphin is best represented by KP 30157, a calvaria with proximal horn cores that differs from KP 71 by its smaller size and less strongly divergent but more strongly compressed horn cores. The horn cores are inserted close together above the orbits on long pedicels. At their base, they are oval in transverse section. They rise upward but diverge gently outward about halfway up and become more strongly mediolaterally compressed in their distal portion. There is slight anticlockwise torsion in the right horn core when viewed from above. The face is strongly angled on the braincase. There is a large

Table 41 Kanapoi *Damalacra* cf. *D. acalla* horn core measurements

		30157	32557
Rt h/c	ap	33.1	33.9
	tr	25.7	26
	lt		
Lt h/c	ap	34.2	
	tr	24.7	
	lt		

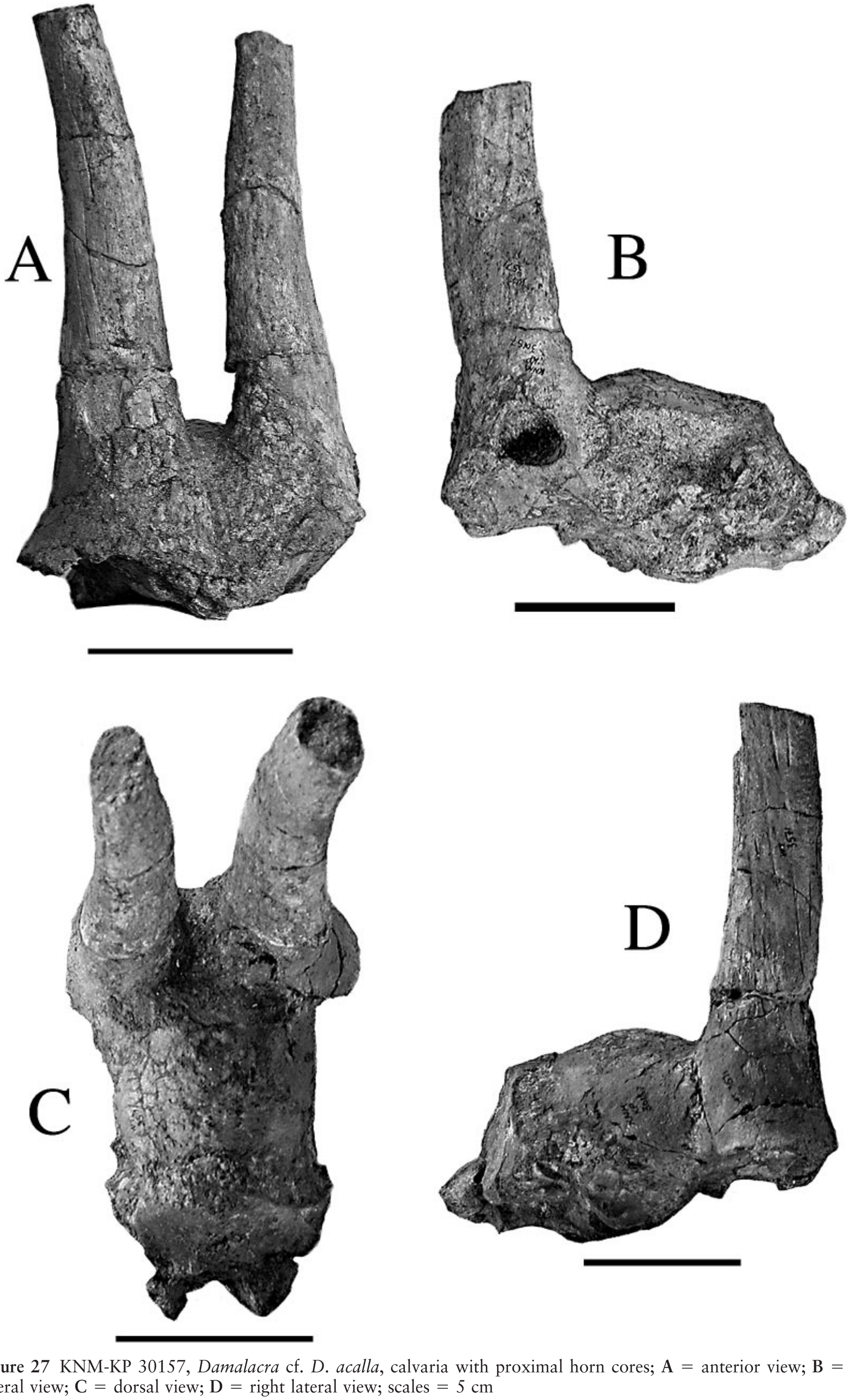

Figure 27 KNM-KP 30157, *Damalacra* cf. *D. acalla*, calvaria with proximal horn cores; **A** = anterior view; **B** = left lateral view; **C** = dorsal view; **D** = right lateral view; scales = 5 cm

Table 42 Kanapoi Alcelaphini tooth measurements

		493	110	111	83	73	31739
M^1	ap		19.8			21.5	18.9
	tr		11.9			15.6	12.5
M^2	ap				26.3		
	tr				22.1		
M^3	ap			30.7		26.5	
	tr			17.1		17.4	
dP_4	ap	22.9					
	tr	8.2					

		387	462	44128
M^1	ap			18.5
	tr			13.3
M^2	ap		24.8	
	tr		13.5	
M^3	ap	27.3	27.7	24
	tr	19.3	17	16.8

		74	108	110	30406	31733	31033	462
P_2	ap					5.9		
	tr					4.5		
P_3	ap					11.1		
	tr					6.6		
P_4	ap					14.9		
	tr					8.2		
M_1	ap					20.6	17.4	
	tr					9.8	9.5	
M_2	ap					25.7		
	tr				10.7	9.8		
M_3	ap		26.3		27.1			
	tr	11.9	9.9	9.5	10.8	9.7		10.2

"*Parmularius*-like" bulge on the top of the braincase, midway between the horn core bases and the nuchal crest.

The shape of the calvaria and horn cores are close to those of *Damalacra acalla* from Langebaanweg but the horn cores would group in size with the smallest *D. acalla* specimens and the calvaria has a much more pronounced parietal boss.

Alcelaphini gen. indet.

(Table 42)

KANAPOI MATERIAL. 73, A = Lt. M^1, B = Rt. M^3; 74, Lt. M_3 frag; 83, Rt. M^2; 108, Rt. M_3; 110, Rt. M_3 frag and Rt. M/; 111, Lt. M^3; 287, Lt. M^3; 462, Rt. M^2, Lt. M^3, Rt. M_3 frag, tooth and bone frags; 493, Rt. dP_4; 30406, Lt. mandible frags (M_{2-3}); 31733, Lt. mandible (P_2–M_3); 31739, Lt. M^1; 311033, Rt. M_1; 44128, Lt. M^3 and tooth frags.

A few alcelaphin teeth were recovered but none were associated with alcelaphin horn cores.

Tribe Aepycerotini

This tribe is today represented by the single but variable species *Aepyceros melampus* (Lichtenstein, 1812). Aepycerotins may be a sister group of the alcelaphins (Vrba, 1984) but the two groups have different habitat preferences and dental morphology. Lyrate horned impalas were the dominant bovid in the Nawata Formation of Lothagam (*Aepyceros premelampus* Harris, 2003b). A smaller and less lyrate-horned species predominated in the middle Pliocene strata of the Shungura, Nachukui, and Koobi Fora Formations but the extant species had become dominant by the late Pliocene.

Aepyceros Sundevall, 1847

Aepyceros sp. indet.

(Figures 28 and 29; Tables 43 and 44)

KANAPOI MATERIAL. 70, prox Rt. h/c; 95, Lt. M^2; 99, prox Lt. h/c; 106, Rt. M^3; 29259, Rt. mandible (M_{1-2}), Lt. M^{2-3}, Rt. M^{1-2}; 29277, calvaria and prox Rt. h/c; 30394, Rt. M; 30417, Lt. M^2; 30418, prox Lt. h/c; 30627, Lt. h/c; 30633, h/c frags; 32543, Lt. h/c; 32544, Rt. mandible (P_4–M_1); 32546, Lt. maxilla (P^2–M^2); 32561, Rt. M^2; 32812, Lt. maxilla frag (M^{1-3}); 32823, Rt. M^2; 36836, Lt. M^1.

KP 29277 is a rather battered calvaria with the proximal portion of the right horn core but it is sufficiently well preserved to confirm the generic identification. The horn cores are mediolaterally compressed at their base with slight lyrate curvature in anterior view and a gentle sigmoid curvature in lateral view. In this regard, the Kanapoi impala more strongly resembles *A. shungurae* Gentry, 1985, from the northern portion of the Lake Turkana Basin (Gentry, 1985; Harris, 1991b) by the lack of lyration than *A. premelampus* Harris, 2003, from the nearby but somewhat older site of Lothagam (Harris, 2003b). The majority of specimens

Table 43 Kanapoi *Aepyceros* sp. indet. horn core measurements

	prox ap (Rt)	prox tr (Rt)	lt (Rt)	prox ap (Lt)	prox tr (Lt)	lt (Lt)
70	42	41				
99				35	30	
29277	37	32				
30418	36	30				
30627				29	23	
32543	33	28				

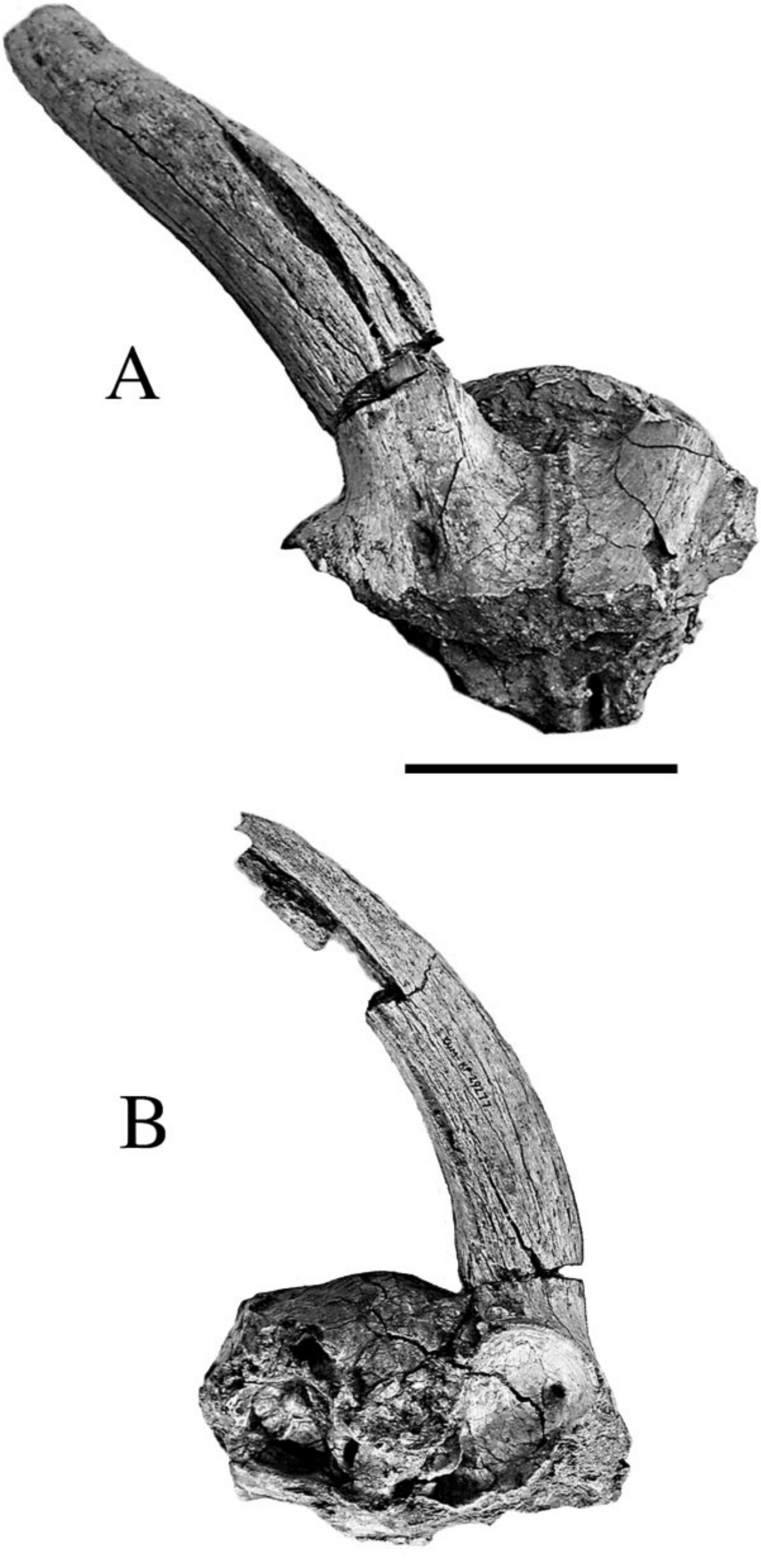

Figure 28 KNM-KP 29277, *Aepyceros* sp. indet., calvaria with proximal right horn core; **A** = anterior view; **B** = right lateral view; scales = 5 cm

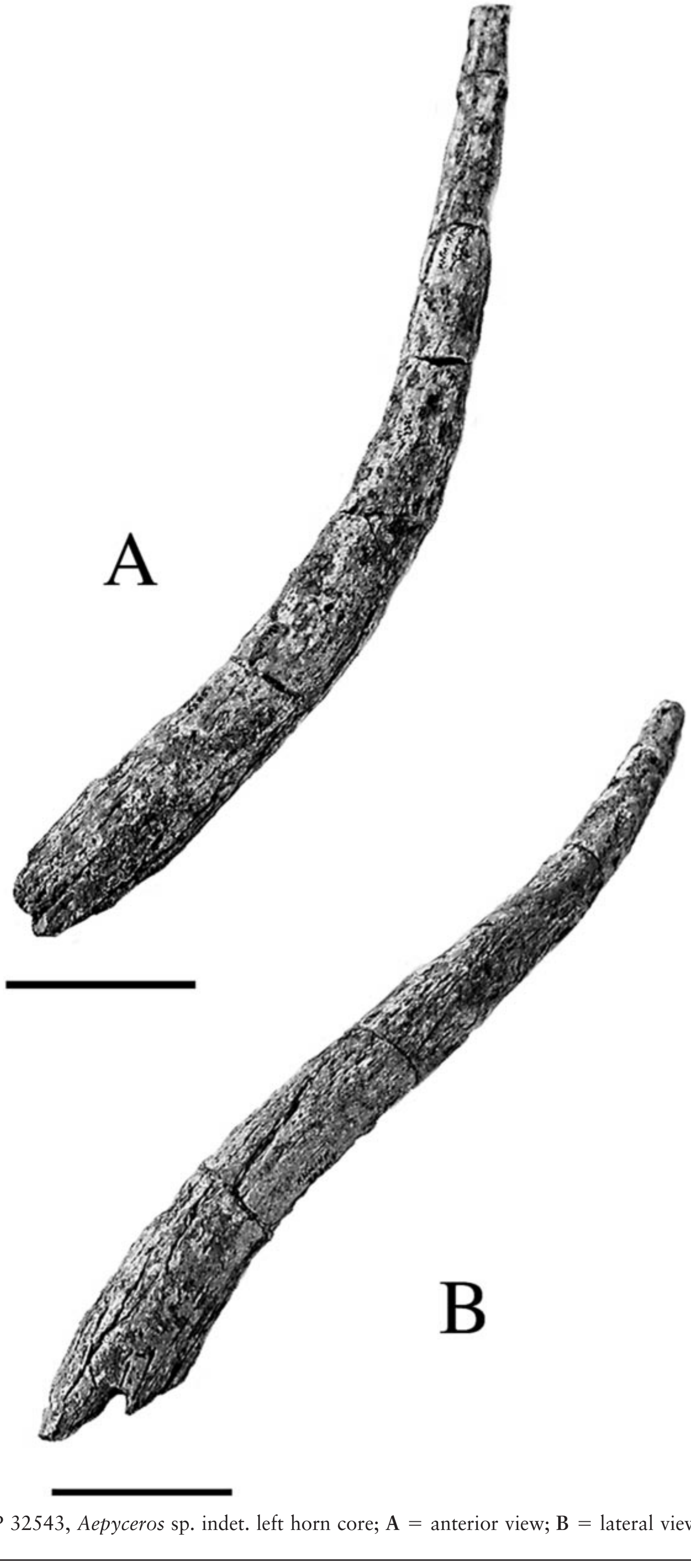

Figure 29 KNM-KP 32543, *Aepyceros* sp. indet. left horn core; **A** = anterior view; **B** = lateral view; scales = 5 cm

Table 44 Kanapoi *Aepyceros* sp. indet. teeth measurements

		95	106	29259L	29259R	30417
M^1	ap				13.5	
	tr				11.1	
M^2	ap	16.6		16.4	16.3	15.3
	tr			13	12.8	11.4
M^3	ap		19.2	18.5		
	tr		11.9	12.3		

		32546	32561	32812	32823
P^2	ap	7.8			
	tr	7.2			
P^3	ap	7.1			
	tr	8.1			
P^4	ap	9.1			
	tr	9.7			
M^1	ap	11.4			
	tr	12.2			
M^2	ap	15.4	16.5	14.5	17.1
	tr	12.7	11.6	13.2	12.5
M^3	ap				
	tr				

		29259R	32544
P_4	ap		8.8
	tr		6.1
M_1	ap	12.1	12
	tr	7.4	8.9
M_2	ap	15.1	
	tr	7.9	
M_3	ap		
	tr		

show slight to moderate transverse annulation; this is most strongly developed in KP 70—the largest specimen whose attribution to *Aepyceros* is slightly less certain than that of the other specimens.

Tribe Antilopini

The Antilopini are small- to medium-sized hypsodont antelopes that appear well adapted to arid areas. The tribe has a long geological history and indeterminate species of gazelles have been reported from the middle Miocene of North (Thomas, 1979) and East Africa (Gentry, 1970).

Gazella de Blainville, 1816

Gazella sp. indet.

(Table 45)

KANAPOI MATERIAL. 29264, Rt. h/c frags; 32513, Lt. and Rt. h/c frags.

Two specimens appear to represent the small and slightly medio-laterally compressed proximal horn cores of an indeterminate species of gazelle.

Table 45 Kanapoi *Gazella* sp. indet. horn core measurements

		29264	32513
Rt h/c	ap	21.5	20.1
	tr	19.3	17.1
	lt		
Lt h/c	ap		19.5
	tr		17.7
	lt		

Tribe Caprini

Caprins, which include domesticated sheep and goats, are documented as common elements of the middle Miocene assemblage from Fort Ternan (Gentry, 1970) but thereafter only appear sporadically in sub-Saharan Africa as rare elements of late Neogene biotas.

Caprini gen. et sp. indet.

(Figure 30)

KANAPOI MATERIAL. 36604, Lt. h/c.

A single, large left horn core with a very pronounced basal sinus may represent an indeterminate species of goat. The horn core is strongly mediolaterally compressed with a flattened lateral surface. It evidently curved backward and outward from the base with a strong lyrate curvature from the anterior view. In some ways, it resembles a large but very flattened impala horn core. At its base, it measures 45.4 mm anteroposteriorly and 31.4 mm transversely.

Tribe Neotragini

Neotragins include about a dozen species of small antelopes that represent the root stock from which the Aegodontia (alcelaphins, antilopins, caprins) emerged (Kingdon, 1982). The tribe is today restricted to Africa. Neotragins representing species of steinbuck and dikdik have been reported from late Miocene assemblages at Lothagam (Harris, 2003b) but their small size tends to make them infrequent components of Pliocene assemblages, although they are known from Langebaanweg (Gentry, 1980) and elsewhere.

Raphiceras H. Smith, 1827

The steenboks (or steinbucks) are moderate-sized neotragins that are distributed discontinuously through open bushland or light woodland in eastern and southern Africa. The horn cores are short to moderately long with little mediolateral compression, inserted widely apart above the back of the orbits, are parallel to one another and, in profile, have a slightly concave anterior edge. Postcornual fossae are present and the supraorbital pits are wide apart (Gentry, 1980).

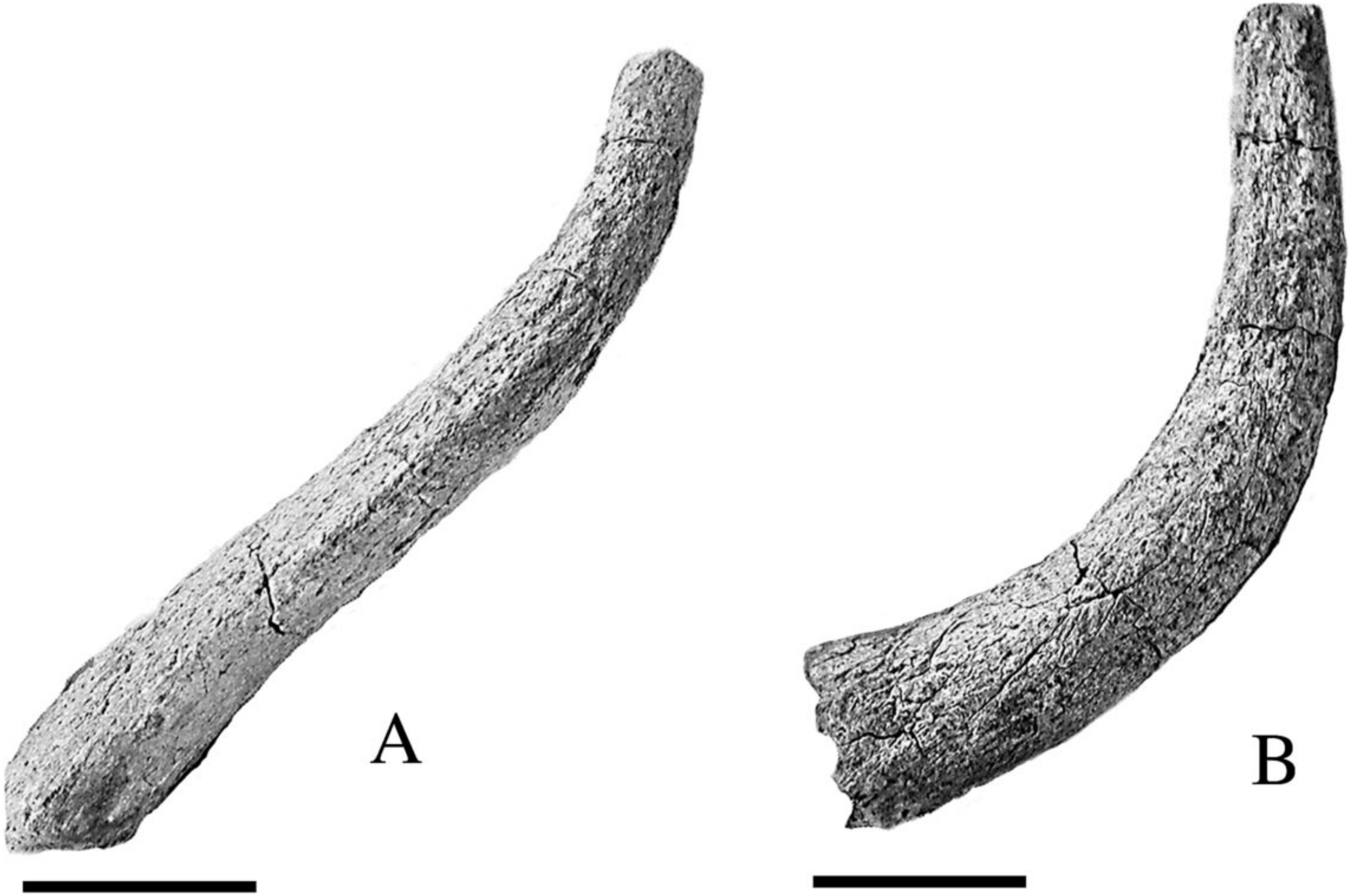

Figure 30 KNM-KP 36604, Caprini gen. and sp. indet. left horn core; **A** = anterior view; **B** = medial view; scales = 5 cm

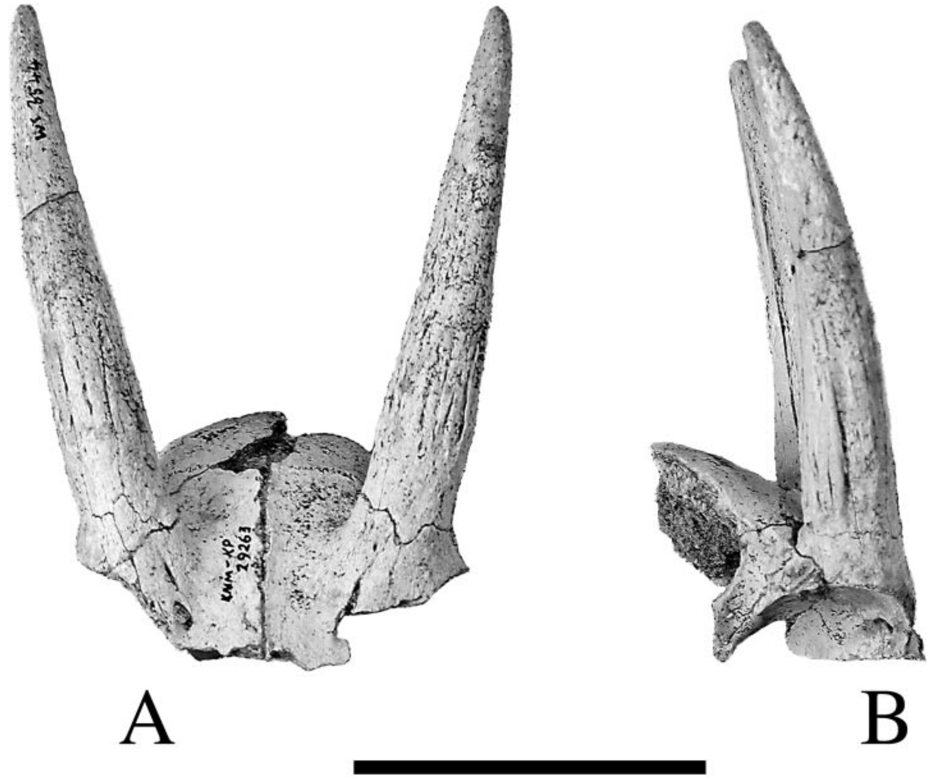

Figure 31 KNM-KP 29263, *Raphiceras* sp. indet. frontlet with horn cores; **A** = anterior view; **B** = right lateral view; scale = 5 cm

Table 46 Kanapoi *Raphiceras* sp. indet. measurements

	29263
Rt h/c ap	14.3
tr	12.7
lt	71.6
Lt. h/c ap	13.7
tr	14
lt	66.6
Width between h/cs	25.2

	93	30443	36833	30273
P_2 ap	4.3			
tr	2.8			
P_3 ap			8.5	
tr			4.5	
P_4 ap		7.5		
tr		4.8		
M_1 ap	10.9	9.5		
tr	6.3	6.2		6.3
M_2 ap	12.0	10.3		10.4
tr	6.6	6.7		7.3
M_3 ap	17.0	16.3		
tr	5.8	6.4		

Raphiceras sp. indet.

(Figure 31; Table 46)

KANAPOI MATERIAL. 93, Rt. mandible (P_2, M_{1-3}); 29263, frontlet with Lt. and Rt. h/cs; 30273, Lt. M_{1-2}; 30443, Lt. mandible (P_4–M_3); 36833, Rt. mandible frag (P_{3-4}).

A frontlet with right and left horn cores (KP 29263) is a little larger than the equivalent portion of an extant steinbuck cranium but is evidently congeneric. A number of neotragine dentitions that are larger than those of dikdiks are interpreted to represent this genus.

Madoqua Ogilby, 1837

The dikdiks are small, shy antelope that occur singly or in pairs in dry bush country in eastern and southwestern Africa. The horn cores are short, often keeled, compressed anterolaterally to posteromedially, and with some flattening of the posteromedial surface. They are inserted wide apart above the back of the orbits, parallel to one another, and not very upright in lateral view. Postcornual fossa are small and shallow but the supraorbital pits are small and wide apart (Gentry, 1987).

Table 47 Kanapoi *Madoqua* sp. indet. tooth measurements

		103	30207	30416	30427	30537	32547
M^2	ap						
	tr						
M^3	ap	9.3			8.2		
	tr	8.6			7.4		
P_2	ap						
	tr						
P_3	ap		4.8				
	tr		3.3				
P_4	ap		6	6.5			
	tr		4.1	3.7			
M_1	ap					7.3	
	tr					4.3	
M_2	ap			7.5		7.2	9.5
	tr			5.1		4.5	5.1
M_3	ap					10.5	11.1
	tr			4.7		5.1	5.1

		36832	36835	36840	30206A	30206B
M^2	ap				6.9	
	tr				8.2	
M^3	ap				8	
	tr				7.6	
P_2	ap					
	tr					
P_3	ap					
	tr					
P_4	ap	8.1		7.5		
	tr	3.9		4.2		
M_1	ap	7.6		7.5	7.3	7.2
	tr	4.6	4.5	4.6	4.7	4.8
M_2	ap		8.9	8.1	8.1	
	tr		5.2	5	5.1	5.2
M_3	ap					
	tr					

Madoqua sp. indet.

(Table 47)

KANAPOI MATERIAL. 103, Rt. M^3; 30206, Rt. mandible (M_{1-2}), Rt. mandible (M_{1-2}), Lt. M^2, Rt. M^3, humerus frags; 30207, Lt. mandible frag (P_{3-4}), prox scapula, dist Lt. and Rt. humerus; 30416, Rt. mandible frags (P_4, M_{2-3}); 30427, Rt. maxilla frag (M^{2-3}); 30537, Lt. mandible (M_{1-3}); 32547, Rt. mandible (M_{2-3}), seven foot bones and distal radius; 36832, Lt. mandible (P_4–M_3); 36835, Rt. mandible (M_{1-2}); 36840, Rt. mandible (P_3–M_2).

Small partial dentitions of comparable size to extant dikdiks represent one of the earliest known species of this genus.

PALEOENVIRONMENTS

Chronologically and stratigraphically, the Kanapoi Formation is equivalent to the lower part of the Nachukui Formation sequence as exposed at Lothagam. The lacustrine interval documented in the middle of the Kanapoi sequence represents a southerly extension of the Lonyumun Lake, which at the nearby locality of Lothagam is represented by the Muruongori Member. The terrestrial sediments at Kanapoi may thus be correlated to an upper portion of the Apak Member and the lower portion of the Kaiyumung Member in the Lothagam succession (Feibel, 2003a). More than fifty mammalian species have been recovered from the Kanapoi Formation (Table 48). The percentage distribution of the larger herbivore families in the Kanapoi biota is broadly comparable with that seen in the Apak Member although the represented taxa suggest a slightly younger age for the Kanapoi assemblage and at Kanapoi large suids seem to have replaced part of the bovid population that dominated at Apak (Table 49).

The Nawata Formation sequence at Lothagam documents the interval of time in which C_4 plants (and particularly grasses) underwent a major expansion in Africa, Asia, and North and South America (Cerling et al., 1997). As documented by Cerling et al. (2003a:fig. 12.5), the $\delta^{13}C$ composition of tooth enamel of mammals with a pure C_4 diet ranges from 1–3 permil whereas that of mammals with a pure C_3 diet in open habitats ranges from -12 to -16 permil. Preliminary results of isotopic analysis of mammalian herbivores from Kanapoi are mostly consistent with the younger radiometric age determinations for the Kanapoi Formation (Table 50). As expected, the elephantoid proboscideans (*Anancus kenyensis, Loxodonta adaurora, Elephas ekorensis*) all had a C_4 grazing diet, as did the suids *Nyanzachoerus pattersoni* and *Notochoerus jaegeri* and the equid *Eurygnathohippus* sp. All these species had assumed a grazing diet before or during the accumulation of the Apak Member at Lothagam. In contrast, C_3 browse was a major component of the diet of deinotheres (*Deinotherium bozasi*), sivatheres (*Sivatherium* cf. *S. hendeyi*), impalas (*Aepyceros* sp.), and ostriches (*Struthio* sp.). The sole rhino tooth analyzed also indicated a browsing diet. The $\delta^{13}C$ content of the fossil ostrich eggshell is more negative than those of extant ostriches from Kanapoi and the $\delta^{18}O$ is more positive; it would appear that there was a greater proportion of C_3 vegetation in the Pliocene ostrich diet compared with that of modern ostriches on the west side of Lake Turkana. Hence, the Lake Turkana Basin in the vicinity of Kanapoi evidently supported a variety of vegetation types and habitats during the early Pliocene. The very positive $\delta^{18}O$ values for the analyzed rhino and sivathere teeth (Table 50) suggests these animals were obtaining most of their water from the plants that they ate.

Wynn (2000) recognized seven types of paleosols at Kanapoi, all of which provide information about the local ecosystem during the process of soil formation.

Table 48 Kanapoi mammalian faunal list

Taxon	Sample size	Body weight	Locomotion	Diet
Chiroptera				
Hipposideros spp.		A	Ae	I
Insectivora				
Myosorex sp.		A	SA	I
Macroscelidae				
Elephantulus sp.		A	SA	I
Lagomorpha				
Leporidae gen. and sp. indet.		C	T	Hg
Rodentia				
Tatera sp.		A	SA	Hb
Murini gen. indet.		A	SA	Hb
Xerus sp.		B	T	HF
cf. *Steatomys* sp.		A	T	Hb
Carnivora				
Enhydriodon ekecaman	1	D	Aq	C
cf. *Torolutra* sp.	1	C	Aq	C
Parahyaena howelli	31	E	T	C
Dinofelis petteri	3	D	T-S	C
Homotherium sp.	4	E	T-S	C
Felis sp.	1	C	T-S	C
Helogale sp.	2	B	T	C
Genetta sp. nov.	3	C	T	C
Primates				
Australopithecus anamensis	59	D/E	TA	O
cf. *Galago* sp. indet.	1	B	A	O
cf. *Ceropithecoides* sp. indet.	6	C	TA	HF
Colobinae sp. A	8	D	TA	HF
Colobinae sp. B	1	D	TA	HF
Parapapio ado	50	D	TA	HF
cf. *Theropithecus* sp.	1	D	TA	HF
Proboscidea				
Deinotherium bozasi	5	H	T	Hb
Anancus kenyensis	2	H	T	Hg
Elephas ekorensis	25	H	T	Hg
Loxodonta adaurora	26	H	T	Hg
Loxodonta exoptata	1	H	T	Hg
Perissodactyla				
Ceratotherium praecox	11	H	T	Hg
Diceros bicornis	4	H	T	Hb
Eurygnathohippus sp. indet.	34	F	T	Hg
Artiodactyla				
Hexaprotodon protamphibius	60	H	Aq	BG
Hexaprotodon sp.	1	H	Aq	BG
Nyanzachoerus pattersoni	77	F	T	Hg
Notochoerus jaegeri	29	F	T	Hg
Notochoerus cf. *N. euilus*	1	F	T	Hg
Giraffa stillei	5	G	T	Hb
Giraffa jumae	1	H	T	Hb
Giraffa sp. indet.	9	G	T	Hb
Sivatherium cf. *S. hendeyi*	3	G	T	Hb
Tragelaphus kyaloae	33	F	T	BG

Table 48 Continued

Taxon	Sample size	Body weight	Locomotion	Diet
Tragelaphini gen. indet.	17	F	T	BG
Simatherium cf. *S. demissum*	4	H	T	Hg
Hippotragini gen. indet.	4	G	T	BG
Kobus sp.	2	F	T	Hg
Reduncini gen. indet.	6	F	T	Hg
Damalacra cf. *D. neanica*	1	F	T	Hg
Damalacra sp. A	5	E	T	Hg
Damalacra cf. *D. acalla*	3	F	T	Hg
Alcelaphini gen. indet.	14	F	T	Hg
Aepyceros sp.	18	F	T	Hb
Gazella sp.	2	D	T	Hg
Caprini gen. and sp. indet.	1	E	T	Hg
Raphiceras sp.	5	D	T	Hb
Madoqua sp.	10	C	T	Hb

Ecovariable categories

Code	Body weight	Code	Locomotor patterns	Code	Feeding preferences
A	0–100 g	T	Terrestrial	I	Insectivore
B	100–1,000 g	TA	Terrestrial–arboreal	F	Frugivore
C	1–10 kg	SA	Semiarboreal	HF	Herbivore–frugivore
D	10–45 kg	A	Arboreal	Hb	Browser
E	45–90 kg	S	Scansorial	Hg	Grazer
F	90–180 kg	TS	Terrestrial–scansorial	BG	Browser–grazer
G	180–360 kg	Aq	Aquatic	C	Carnivore
H	360+ kg	Ae	Aerial	CI	Carnivore–insectivore
		F	Fossorial	O	Omnivore
		TF	Terrestrial–fossorial		

1. Modern analogues of the Aberegaiya paleosols are found throughout semiarid regions of East Africa on floodplains flanking large river systems and support edaphic savanna grasslands within low tree–shrub savanna mosaics.
2. The Lorenyan paleosol is found in delta deposits where it represents brief emergence of the delta flats and desiccation of the clayey parent material; modern analogues occur on the Omo River Delta at the north end of Lake Turkana where they support sparsely vegetated grasslands with variable admixtures of ephemeral forbs.
3. Dite paleosols, from which most of the hominid fossils were derived, were better drained but formed in broadly similar conditions to the Aberegaiya and Lorenyang paleosols. Modern analogues to the Dite paleosols are found in the lower Omo Valley, where well-drained soils support low tree–shrub savanna vegetation in semiarid to arid climatic regimes.
4. Abilat paleosols are calcic xerosols. Their characteristics are intermediate between Dite and Aberegaiya paleosols and they are believed to represent transitional habitats between these two pedotypes. Vegetation growing on Abilat soils would thus have been transitional between the forb-dominated edaphic grasslands of the Aberegaiya pedotype and the low tree–shrub savanna of the Dite pedotype.
5. The Nasua paleosol is found on delta sediments. Like the Lorenyang, the Nasua paleosol represents brief emergence of the delta flats but supported denser vegetation; similar modern clayey soils are found on the Omo Delta, where they support shrub thickets of aquatically adapted *Acacia* and *Cadaba* species.
6. Kabisa paleosols with vertical rhizoliths are found in channel sandstones in the upper fluvial series; modern counterparts in the lower Turkana Basin occur in the sandy soils of ephemeral channels, where they support gallery woodland and thicket vegetation—often dominated by *Acacia tortilis*.
7. Akai–Ititi paleosols have horizontal rhizoliths representing root mats in nearshore environments where groundwater is shallow; modern analogues fringe the Omo Delta and support lakeside and streamside grasslands with root mats of *Phragmites*, *Typha*, and *Cyperus* species and *Loudetia phragmatoides* or *Sporobolis spicatus*.

Wynn's (2000) overall interpretation of the prevailing habitats at Kanapoi was that they strongly resembled habitats that presently occur in the re-

Table 49 Percentage distribution of large herbivores at Lothagam and Kanapoi

	Lr Nawata	Ur Nawata	Apak	Kanapoi	Kaiyumung
Elephantoidea	4.73	1.97	11.26	13.95	1.52
Rhinocerotidae	4.73	5.90	5.30	4.26	6.06
Equidae	10.11	11.52	8.61	8.04	13.64
Hippopotamidae	20.65	18.54	12.58	14.42	0.00
Suidae	24.52	18.82	13.25	25.06	36.36
Giraffidae	2.80	2.53	5.96	4.26	4.55
Bovidae	32.47	40.73	43.05	30.02	37.88
	100.00	100.00	100.00	100.01	100.00

Table 50 Results of stable isotope analysis of Kanapoi herbivores

	$\delta^{13}C$	$\delta^{18}O$
Struthio sp.		
WT 3597	−8.66	10.89
Anancus kenyensis		
KP 30442	−0.13	−1.11
Elephas ekorensis		
KP 30173	−1.74	−1.32
WT 3570	−1.48	2.37
Loxodonta adaurora		
KP 390	−2.73	0.87
30196	−2.5	1.05
30196	−2.34	1.09
30596	−1.08	2.2
KP 383	−2.99	−0.36
Deinotherium bozasi		
WT 3617	−12.43	−1.75
Rhinocerotidae gen. indet		
WT 3223	−9.98	4.71
Eurygnathohippus sp.		
30233	1.24	2.09
Nyanzachoerus pattersoni		
KP 205	−6.5	1.19
WT 3222 (M_3)	−1.94	1.14
KP-X10	−1.19	−0.22
Notochoerus jaegeri		
KNM-3348 B	−1.74	1.43
KP 241	−2.01	1.07
KP 265	−5.47	−2.19
WT 3227	−1.74	1.78
Sivatherium cf. *S. hendeyi*		
KP 30227	−9	8.6
Aepyceros sp.		
WT 3240-Aepy	−10.02	1.36
WT 3240	−9.77	1.46

gion of the modern Omo River Delta at the north end of Lake Turkana. Most of the hominids derive from Dite paleosols that he interpreted to have supported low tree–shrub savanna vegetation in a semiarid climate with an annual rainfall that ranged from 350 to 600 mm. Wynn (2000) suggested that Kanapoi may represent the earliest known occurrence of hominids venturing into relatively open habitats. However, Ward et al. (1999) caution that many of the hominid specimens show evidence of carnivore damage. Thus, it is possible that the hominid remains were transported by carnivores to the locations where they accumulated. Other paleosols ranged from poorly drained Vertisols with forb-dominated edaphic grassland in local shallow depressions to well-drained alluvial soils supporting gallery woodland adjacent to stream courses. The proportion of soil carbonate contributed by C_4 plants (i.e., grasses) ranges from 25% in the Kabisa paleosol to 40% in the Dite and Abilat paleosols (Wynn 2000).

Confirmation of the nature of the terrestrial habitats during the interval that the early Pliocene assemblage accumulated at Kanapoi is provided by the dietary adaptations of the terrestrial vertebrate fossils (Table 48). Proboscideans amount to about 14% of the large vertebrate biota: *Loxodonta adaurora* and *Elephas ekorensis* predominate, whereas *Anancus* and *Deinotherium* are only sparsely represented. Elephantids and gomphotheres had acquired a grazing diet by the beginning of the Pliocene and their presence at Kanapoi appears to signify open habitat in the near vicinity of the Kanapoi Delta, although the presence of *Deinotherium* confirms an ample supply of C_3 vegetation. Rhinos were represented by the predecessors of the two extant African species, both of which had acquired their different (grazing versus browsing) dietary specializations by the beginning of the Pliocene. Equids are represented by *Eurygnathohippus,* a grazing hipparionine. Large suids are represented by *Nyanzachoerus pattersoni* and *Notochoerus jaegeri*; both were interpreted as closed habitat species by Bishop (1994) on the basis of their postcranial anatomy but both species were evidently specialized grazers on the basis of the isotopic composition of their tooth

Table 51 Stratigraphic distribution of bovid tribes at Lothagam and Kanapoi

	Lr Nawata	Ur Nawata	Apak	Kanapoi	Kaiyumung
Tragelaphini	3.33	2.08	20.63	39.37	16.00
Bovini	1.33	2.08	9.52	3.15	28.00
Boselaphini	24.67	7.64	3.17		
Hippotragini	5.33	5.56	4.76	3.94	
Reduncini	11.33	21.53	9.52	7.09	8.00
Alcelaphini	4.67	17.36	14.29	18.11	12.00
Aepycerotini	48.00	40.28	31.75	14.17	36.00
Antilopini	0.67	1.39	4.76	2.36	
Neotragini	0.67	2.08	1.59	11.81	
	100.00	100.00	100.00	100.00	100.00

enamel (Harris and Cerling, 2002; Cerling et al., 2003b). Giraffids were relatively uncommon constituents of the Kanapoi assemblage but both sivatheres and giraffines were C_3 browsers at that point in time. Bovids, as usual, are the most commonly encountered terrestrial herbivores. Tragelaphins, aepycerotins, and neotragins—now all closed habitat or forest-edge forms—make up two thirds of the Kanapoi bovid assemblage, but the presence of bovins, reduncins, hippotragins, and alcelaphins is indicative of nearby sources of grass. In contrast with the bovid assemblages from the Apak and Kaiyumung Members, the Kanapoi bovid assemblage has more tragelaphins and alcelaphins but fewer bovins and aepycerotins—which may be interpreted to represent drier and less wooded habitats in the vicinity of Kanapoi (Table 51). Overall, grazing species outnumber browsing species by a ratio of nearly two to one; in terms of numbers of individuals, browsers out-

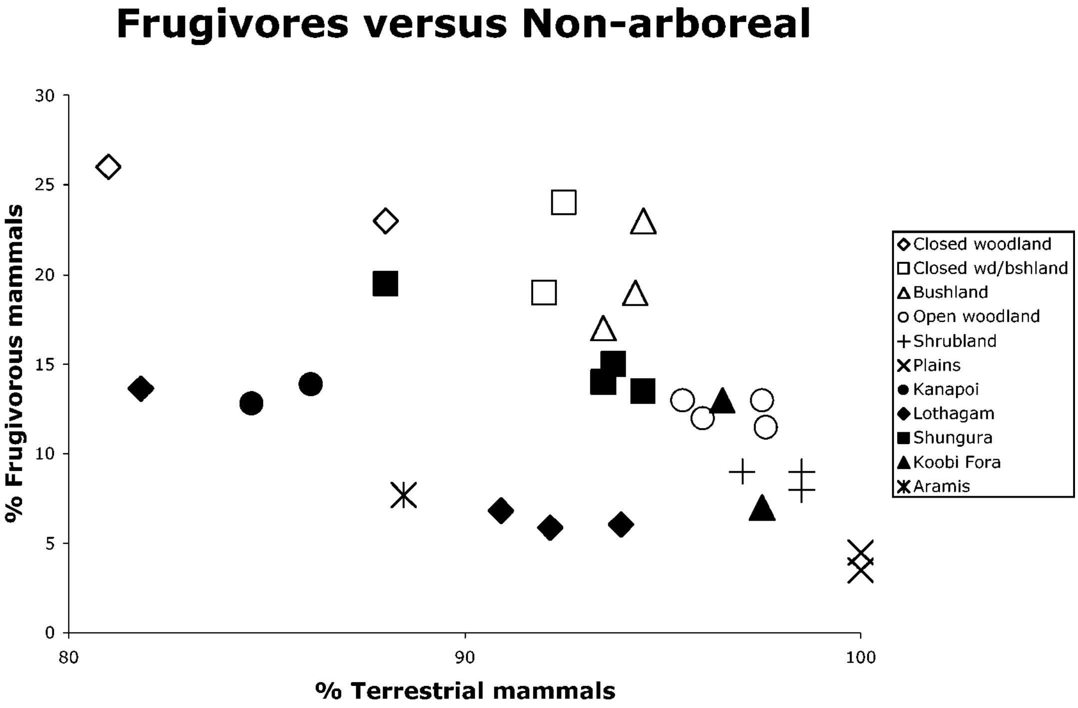

Figure 32 Graph depicting ecological structural analysis of frugivorous mammals and nonarboreal mammals from modern African habitats and from Pliocene assemblages from the Lake Turkana Basin. Data for extant habitats and assemblages from the Shungura and Koobi Fora Formations are from Reed (1997); those for Lothagam assemblages are from Leakey and Harris (2003); those for Aramis are from WoldeGabriel at al. (1994). Of the two data points representing Kanapoi, that on the right is for the assemblage from below the lacustrine interval, that on the left is for the assemblage from above the lacustrine interval

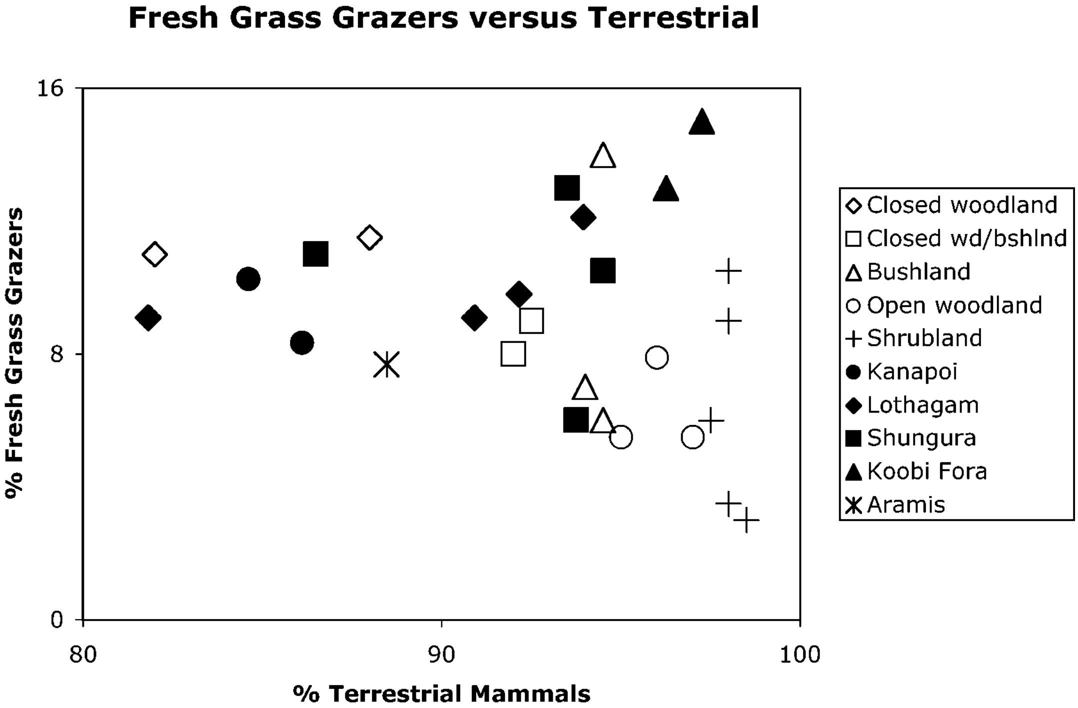

Figure 33 Graph depicting ecological structural analysis of fresh grass grazing mammals and terrestrial mammals from modern African habitats and from Pliocene assemblages from the Lake Turkana Basin. Data points as for Figure 32

number grazers by three to one. In confirmation, the Kanapoi small mammals suggest a relatively dry climate and open habitat (Appendix).

The Kanapoi large-mammal assemblage shares many elements with that from the 4.4 Ma site of Aramis, Ethiopia (WoldeGabriel et al., 1994), although, with the exception of the primates, most of the Aramis fossil material has yet to be described in detail. Taxa shared by Kanapoi and Aramis include elephantids (unidentified at Aramis), *Anancus, Deinotherium, Ceratotherium* cf. *C. praecox,* "*Hipparion*" sp., *Hexaprotodon* sp., *Nyanzachoerus pattersoni, Notochoerus jaegeri,* a large and small species of *Giraffa,* and tragelaphins, bovins, and neotragins. However, with the exception of an unidentified kudu (*Tragelaphus* sp.), large vertebrates are rare at Aramis, as are aquatic vertebrates. WoldeGabriel et al. (1994) interpret the dominance of colobines and kudus at Aramis to be a strong indication of a closed, wooded environment. However, the presence at an early Pliocene site of elephantids, *Anancus, Ceratotherium,* an equid, a hippo, *Nyanzachoerus, Notochoerus,* and bovins is indicative of a diverse open-country grazing component in the biota. Moreover, the larger genera of early Pliocene colobines were more terrestrial than their extant counterparts (Leakey et al., 2003) and hence the dominance of colobines may not necessarily mandate the presence of closed woodland. As at Aramis, tragelaphins were the most abundant bovids recovered from Kanapoi. However, in contrast with the situation at Aramis, papionin primates far outnumbered the colobines. On balance, Kanapoi would appear to represent habitats that were similar to but more open than those of Aramis. Andrews and Humphrey (1999) stated that the fossil assemblages from both Aramis and Kanapoi are underrepresented by small mammals that often provide a more precise assessment of the prevailing paleoenvironments than do large migratory species. Large quantities of micromammals that were retrieved by the National Museums of Kenya expeditions have yet to be studied in detail (see Appendix) and the bulk of the nonprimate component of the Aramis fauna has also yet to be studied in depth.

Ecological diversity provides a different means from taxonomic uniformitarianism for analyzing the community structure of fossil mammalian faunas in order to obtain information about the habitats represented by faunal assemblages (Andrews et al., 1979). Using this methodology, Andrews and Humphrey (1999) interpret the Kanapoi material collected by American expeditions in the 1960s, as ". . . dominated by medium- to large-sized terrestrial species and both browsers and grazers are well represented. The high terrestrial component in the fauna places it with the drier end of the present-day woodland and bushland ecosystems suggesting open woodland with abundant grass."

Ecological structural analysis as formulated by Reed (1997) provides a different interpretation. Reed established that habitats were predicted by locomotory adaptations and characterized by trophic ecovariables and found that it was possible to differentiate between different terrestrial habitats by plotting the percentage of frugivorous mammals against the percentage of nonarboreal mammals (Reed, 1997:fig. 5A). Similar results were obtained by plotting the percentage of fresh grass grazers against percentage of terrestrial mammals and this also established the presence/absence of edaphic grassland (Reed, 1997:fig. 5B). The estimated body weights, locomotor adaptations, and feeding preferences for the Kanapoi mammals are listed in Table 48. When Pliocene assemblages from the Lake Turkana Basin are superimposed on the modern habitat plots for frugivores versus nonarboreal mammals (Fig. 32), the two Kanapoi assemblages (above and below the Lonyumun Lake incursion) plot with the closed woodland assemblages. A similar grouping occurs when the Kanapoi assemblages are superimposed on the graph of fresh grass grazers versus terrestrial mammals (Fig. 33). In both cases, the Kanapoi assemblages plot close to those from the Kaiyumung Member at Lothagam and Shungura Member B in the lower Omo Valley. The reason why the Kanapoi assemblages appear to indicate closed woodland is because the primates have been interpreted as at least partly arboreal (requiring shelter in trees at night). Attribution of terrestrial adaptation to one or more of the primate species would skew the sample toward an interpretation of more open habitat. Given that the hominin was bipedal and that early Pliocene cercopithecoids were more terrestrial than later forms, such an interpretation would be more in keeping with the dietary adaptations of the fossil species and the ecological adaptations of their modern counterparts.

SUMMARY

The early Pliocene site of Kanapoi, southwest of Lake Turkana in northern Kenya, has yielded the oldest australopithecines from eastern Africa although a similar age has recently been claimed for a new australopithecine locality in southern Africa (Partridge et al., 2003). Associated with the hominin remains from Kanapoi is a diverse vertebrate fauna that has been recovered from fluvial and lacustrine sediments dating between 4.17 and 4.07 Ma. The Kanapoi tetrapod fauna is much more prolific than that from any other similarly aged locality elsewhere in the Lake Turkana Basin (Nachukui and Koobi Fora Formations). The assemblage includes 24 species of fish, 7 species of chelonians, 4 species each of crocodylians and birds, and over 50 species of mammals. Few of the recognized species are new but micromammals have not yet been thoroughly investigated. Relatively complete suid specimens mandate the transfer of the species *Nyanzachoerus jaegeri* to the genus *Notochoerus.* Paleosols associated with the fauna remains suggest a mixture of open and closed habitats similar to those currently found in the vicinity of the Omo Delta at the north end of Lake Turkana. Such an interpretation is supported by the dietary adaptations of the herbivorous fossil mammals and the habitats exploited by their living representatives.

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APPENDIX

PRELIMINARY ASSESSMENT OF THE KANAPOI MICROMAMMALS

ALISA J. WINKLER

Order Chiroptera

Family Hipposideridae

Hipposideros Gray, 1831

Hipposideros spp.

Winkler (1998) reported a large and small species of *Hipposideros* (Old World leaf-nosed bats), represented mainly by postcrania and isolated teeth, from the "Bat Site" locality (WT 3409). In Africa, *Hipposideros* is currently known from seven superspecies or species groups (Kingdon, 1974). *Hipposideros* may roost in a variety of shelters, including caves, holes in the ground, hollow trees, and in undergrowth. Several species are known to roost with other species of bats. The size of roosting aggregations varies from several to over 1,000 individuals. At the "Bat Site" locality, the large concentration of bats, relative scarcity of other taxa, and little evidence of alteration or transport of the bones and teeth suggest that this assemblage represents an attritional accumulation under a roost site.

Order Insectivora

Family Soricidae

Subfamily Crocidurinae

Crocidurinae gen. and sp. indet.

Two incomplete mandibles of shrews are currently known from Kanapoi. At least one of these may be referable to *Myosorex* Gray, 1838. This genus is known from Africa at present and is also reported from the African Plio–Pleistocene (Hendey, 1981; Wesselman, 1984).

Order Macroscelidea

Family Macroscelididae

Elephantulus Thomas and Schwann, 1906

Elephantulus sp.

Three specimens of *Elephantulus* have been recovered so far from Nzube's Mandible Site (WT 3227). Kanapoi includes one of the earliest known records of the genus, the other being Langebaanweg (Hendey, 1981). The present range of *E. rufescens* (Peters, 1878) (spectacled or long-eared elephant shrew) includes thickets in South Turkana (Coe, 1972).

Order Lagomorpha

Family Leporidae

Leporidae gen. and sp. indet.

Dental and postcranial remains of lagomorphs are known from Nzube's Mandible Site and several other sublocalities at Kanapoi. Lagomorphs are well represented in modern and fossil African faunas.

Order Rodentia

Winkler (1998) reported a rich microvertebrate fauna associated primarily with the locality that yielded the holotype mandible of *Australopithecus anamensis* (Nzube's Mandible Site). Recovered materials included cranial and postcranial remains of fish, amphibians, reptiles, birds, and mammals. The microvertebrates from Nzube's Mandible Site likely represented a concentration of owl pellets, with some attritionally incorporated taxa. The mammalian specimens were dominated by a small species of the gerbil *Tatera* Lataste, 1882, and by murine rodents. There is also a new species of ground squirrel (*Xerus*) Hemprich and Ehrenberg, 1832, and a new dendromurine genus that appears to be the sister taxon to *Steatomys* Peters, 1846, (fat mice). Although the Kanapoi rodents have yet to be studied in detail, the fauna appears most similar to that from the lower Shungura Formation of the lower Omo Valley (Wesselman, 1984). At the generic level, the Kanapoi rodents are strikingly similar to those present today in the South Turkana region (Coe, 1972). Based on a comparison with modern analogues, the Kanapoi small mammals suggested a relatively dry climate and open habitat.

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Carnivora from the Kanapoi Hominid Site, Turkana Basin, Northern Kenya

Lars Werdelin[1]

ABSTRACT. Kanapoi is the earliest Pliocene site yet described in eastern Africa with a substantial carnivoran record. It includes eight species in as many genera, representing five families. The material is dominated by the hyaenid *Parahyaena howelli* n. sp., but also includes a new *Enhydriodon* species, *E. ekecaman,* the lutrine cf. *Torolutra* sp., the felids *Dinofelis petteri, Homotherium* sp., and *Felis* sp., the herpestid *Helogale* sp., and the viverrid *Genetta* n. sp. The Kanapoi Carnivora includes the remains of the first post-Miocene radiation of endemic African Carnivora.

INTRODUCTION

The earliest Pliocene (here taken as ca. 5.2–4.0 Ma) has provided relatively few eastern African localities containing mammalian fossils compared with the million years that followed. Most of the localities that do exist from this time interval have either few carnivores associated with them or are as yet undescribed. Thus, the Apak Member at Lothagam includes only four carnivore taxa (Werdelin, 2003), the Lonyumun Member of the Koobi Fora Formation three (Werdelin and Lewis, unpublished), the Kataboi Member of the Nachukui Formation and Kosia (also West Turkana) also three (personal observations). Outside of Kenya, localities of this time period from Uganda have also yielded few carnivores (Petter et al., 1991). A richer site is Aramis, in Ethiopia, although the carnivores there have yet to be described (Howell, personal communication). Kanapoi, with its somewhat larger sample of carnivores, thus adds significantly to our knowledge of carnivoran evolution in the earliest Pliocene of eastern Africa.

The bulk of the material discussed herein was obtained by the National Museums of Kenya expeditions to Kanapoi in the early 1990s. However, a few carnivore specimens were recovered by the earlier American expeditions. These have been mentioned a few times in the literature under various guises (Behrensmeyer, 1976; Savage, 1978; Howell and Petter, 1980; Turner et al., 1999). In particular, Behrensmeyer (1976) lists *Enhydriodon* n. sp., *Hyaena* sp., and Machairodontinae indet. as present at Kanapoi. Of these, the first is here still referred to *Enhydriodon* Falconer, 1863, the second to *Parahyaena* Hendey, 1974, while the third is here listed as Carnivora indet., as it cannot be determined if the specimen belongs to *Dinofelis* Zdansky, 1924, or *Homotherium* Fabrini, 1890. The remaining taxa described below are new to the Kanapoi fauna.

CONVENTIONS AND ABBREVIATIONS

Kanapoi fossils in the collections of the National Museums of Kenya are formally accorded the acronym KNM-KP before the accession number; to save repetition, this acronym is omitted from the lists of Kanapoi specimens and abbreviated to KP in the body of the text.

Tooth abbreviations in upper case (I, C, P, M) indicate upper teeth; those in lower case (i, c, p, m) indicate lower teeth. Hence M1 is the upper first molar, p4 is the lower fourth premolar. The following abbreviations are used in the text and tables:

a-p = anteroposterior
Dist = distal
L = anatomical length (long bones); mesiodistal length (teeth)
LpP_4 = length of main cusp of P_4
MC = metacarpal
MT = metatarsal
max = maximum
min = minimum
Prox = proximal
Sust = sustentaculum
transv = transverse
W = buccolingual width
WaP^4 = anterior width (including protocone) of P^4
$WblP^4$ = minimum blade width of P^4

SYSTEMATIC DESCRIPTION

Order Carnivora

Family Mustelidae

Generally speaking, mustelids are rare in the fossil record of eastern Africa. For the most part, this may reflect a preservational bias against smaller species of Carnivora. However, those localities that are particularly rich in smaller Carnivora also differ among themselves in the richness and diversity of their mustelids. Thus, Hadar is rich in small mustelids (personal observations), while Olduvai has fewer taxa, despite the smaller Carnivora being well represented at the latter site (Petter, 1973).

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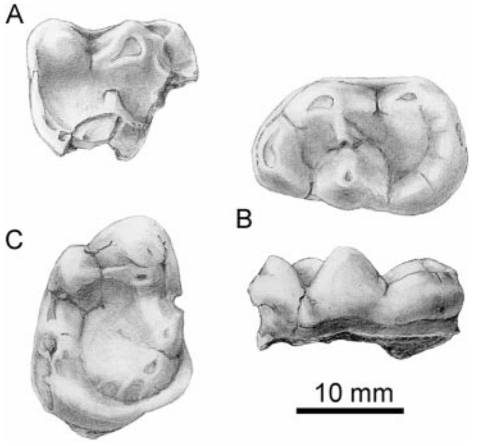

Figure 1 *Enhydriodon* n. sp., **A,** KP 10034A, right P4 in occlusal view; **B,** KP 10034B, right m1 in (top) occlusal and (bottom) lingual view; **C,** KP 10034C, right M1 in occlusal view. In **A** and **C,** anterior is to the right; in **B,** anterior is to the left

This variation may reflect real differences in paleoecology between the sites. Nevertheless, the majority of mustelids found in the eastern African fossil record are larger species of the genera *Mellivora* Storr, 1780, *Enhydriodon* and *Torolutra* Petter, Pickford, and Howell, 1991. Kanapoi is no exception to this pattern, with both of the latter genera represented.

Enhydriodon Falconer, 1863

The genus *Enhydriodon* encompasses a number of species of Enhydrini (sea otters) of large to very large size. The genus is known from the Siwaliks of Pakistan and India, where it was first described (Lydekker, 1884; Willemsen, 1992). However, the main diversity within *Enhydriodon* is found in Africa, with several species of varying size known from a number of localities dating between ca. 6.0 Ma (Lukeino Formation; Pickford, 1978) and ca. 2.5 Ma (Omo, Shungura Formation Members E+F; Howell and Petter, 1976). The Kanapoi material represents one of the earlier members of this lineage.

Enhydriodon ekecaman sp. nov.

(Figure 1)

Enhydriodon n. sp. Behrensmeyer, 1976
Enhydriodon pattersoni Savage, 1978 (nomen nudum)
Enhydriodon pattersoni Turner, Bishop, Denys, and McKee, 1999 (nomen nudum)

DIAGNOSIS. Differs from Siwalik *Enhydriodon* in its smaller size. Differs from *E. africanus* Stromer, 1931 (the other described African *Enhydriodon*) by having a broader m1 with a more open talonid basin and relatively smaller paraconid, more robust and larger M1 hypocone(s) and more stoutly built P4.

HOLOTYPE. KNM-KP 10034, A = right P4 (Fig. 1A), B = right m1 (Fig. 1B), C = right M1 (Fig. 1C), D = right C). Written documentation regarding the association in the field of these four specimens was provided by Dr. J. C. Barry (in correspondence). Given this information, it is reasonable to assume that all four belonged to a single individual and therefore the entire hypodigm is chosen as the holotype of this new species.

ETYMOLOGY. After the Turkana "ekecaman," meaning fisherman. The diet of this animal was composed at least in part of fish.

KANAPOI MATERIAL. 10034; associated teeth (holotype).

MEASUREMENTS. KP 10034A, buccal length = 16.5; KP 10034B, total length = 21.2, trigonid length = 11.5, talonid length = 9.3, trigonid width = 13.3, talonid width = 13.5; KP 10034C, buccal length = 12.1, lingual length = 15.8, anterior width = 19.8, posterior width = 19.0. Measurements defined as in Willemsen (1992).

The right upper carnassial, KP 10034A (Fig. 1A), is missing the protocone and most of the hypocone and posterior shelf. The parastyle is short and low but has a distinct anterior cusp. The paracone is high and much the largest buccal cusp. There are blunt crests leading anteriorly to the parastyle, anterolingually toward the protocone and posteriorly toward the metacone. The latter crest is interrupted by a shallow valley before it meets the metacone. The latter cusp is set far posteriorly and is much lower and smaller than the paracone. There was an extensive basin formed posterobuccally to the hypocone and the posterobuccal corner and posterior margin of the tooth lie at nearly right angles to the anteroposterior axis of the tooth. The cingulum extends along the entire preserved part of the tooth except for the posterobuccal corner.

The right lower carnassial, KP 10034B (Fig. 1B) is low, broad, and stoutly built. The three trigonid cusps are all low and pyramidal with their major axes directed either anteroposteriorly (protoconid, metaconid) or transversely (paraconid). In occlusal view, the paraconid is the smallest of the three cusps but all three are worn down to about the same height. The apex of the paraconid is set slightly lingual to the middle of the cusp and it is also slightly broader lingually than buccally. The apex of the protoconid is set slightly anterior to the middle of the cusp. There is a blunt crest that runs down the lingual side of this cusp toward the talonid, making the cusp almost diamond-shaped, though with a gently curved buccal side. Anteriorly, the protoconid is separated from the paraconid by a shallow valley. Posteriorly, the accessory protoconid cusp is very weakly developed, merely forming a low bulge on the posterior face of the cusp. The metaconid is set slightly posterior to the protoconid. Its apex is at the middle of the cusp. The cusp is triangular in occlusal view, with the apex of the triangle directed toward the buccal side. Anteriorly, the metaconid is separated from the paraconid by a deep valley. Between the trigonid cusps is formed a shallow, flat basin that is about 3 mm wide and 2 mm long. The talonid basin is low and wide. The entoconid is well developed but low. In occlusal view, it is about the size of the paraconid. None of the other talonid cusps is well defined. Instead, they form a low, broad, gently undulating ridge surrounding the central basin. The buccal cingulum is strong and extends from the anteriormost part of the tooth to the posterior end of the hypoconid.

The right M1, KP 10034C (Fig. 1C), is broad, low, and robust, with a very broad lingual basin. The paracone is small, and buccal to it, there is a large parastyle, which is in fact larger than the paracone itself. The paracone is low and worn and connected to the metacone by a narrow valley. The metacone is considerably higher and larger than the paracone and has a pyramidal base. It is set at the posterior margin of the tooth. Lingual to the metacone and separated from it by a narrow valley there is a metaconule that is almost as large as the metacone itself. This cusp is also set at the posterior margin of the tooth. Lingual to the metaconule there is a wear facet for occlusion with m2. This wear facet is confined to the posterior margin of the tooth. At the posterolingual corner of the tooth there is a large swelling of the cingulum, forming a low cusp. The protocone is double, with one cusp set slightly anterobuccal to the other. These two cusps are of about equal size. The cingulum runs around the entire tooth, except anteromedially, where it is worn down by the wear facet for P4, and posterolingually, where the aforementioned m2 wear facet is located. The cingulum is otherwise weakest around the metacone.

The right C, KP 10034D, is short and straight, with a crown that is only slightly longer than it is wide. The tip is worn flat. There is a strong medial cingulum but no lateral one.

DISCUSSION. The material of *Enhydriodon* from Kanapoi is limited, but can nevertheless be distinguished from other African *Enhydriodon* of similar age. The lower carnassial, for example, differs from that of *E. africanus* from Langebaanweg among other features in being shorter and relatively wider, in the somewhat more widely spaced trigonid cusps, and in the flatter and more open talonid basin (cf. Hendey, 1978b). The development of the posterolingual cusplets is more pronounced in the Kanapoi form. The M1 differs from a partial M1 from Kosia (West Turkana, ca. 4.0 Ma) in that the anterolingual corner of the Kanapoi M1 forms a nearly right angle, while the homologous angle of the Kosia tooth is closer to 135 degrees (personal observations). The Kanapoi *Enhydriodon* further differs from younger *Enhydriodon* from formations such as Hadar, Koobi Fora, and Shungura in its much smaller size. Hence, we can infer that the Kanapoi *Enhydriodon* belongs to a hitherto unknown species of that genus, a species that is not at present known from any other site. All four *Enhydriodon* teeth from Kanapoi originate from the American expeditions (1966–72) and were collected in 1967.

Torolutra Petter, Pickford, and Howell, 1991

Torolutra is a genus of otters similar in size to the living European otter *Lutra lutra* (Linnaeus, 1758), or slightly larger. Only a single species, *T. ougandensis,* has been described (Petter et al., 1991). This material is from Nyaburogo and Nkondo in Uganda, while the species has also been tentatively identified from Ethiopia in the Usno Formation of the Omo Group. These localities bracket Kanapoi in age.

cf. *Torolutra* sp.

KANAPOI MATERIAL. 30155, right I3, left and right P4 fragments, premolar fragment, m1 talonid fragment, proximal left radius fragment, proximal right tibia fragment, humerus shaft fragment, partial cervical, thoracic and caudal vertebrae, assorted indeterminate fragments.

The I3 is strongly recurved and has a short crown. The enamel reaches farther down on the lateral than on the medial side. There is a prominent cingulum surrounding this tooth. This cingulum is best developed on the medial side. The root of I3 is relatively straight. The P4 preserves the metastyle, a partial paracone and a part of the lingual protocone shelf. There is no carnassial notch. The protocone shelf is not as long as in *Enhydriodon,* being instead more similar to that of *Lutra* Brisson, 1762. The m1 preserves the posterior part of the talonid, with a prominent hypoconid and low bumps indicating entoconulid and entoconid. The cingulum is prominent around the posterior end of the tooth. The proximal radius fragment is small and broken. The proximal tibia fragment shows only parts of the proximal articular surface. All the vertebrae are relatively robust, the proximal caudal vertebra extremely so, while the cervical vertebrae are relatively much smaller.

DISCUSSION. These specimens compare well, as far as comparisons can be made, with specimens of *Torolutra ougandensis* described by Petter et al. (1991). They are a little larger than the specimens from Uganda, but match the Omo specimens figured by those authors quite well.

Family Hyaenidae

Hyenas are common elements in eastern African Mio–Pliocene faunas. As in Eurasia, there is an extinction event at the end of the Miocene that eliminates the dominant ‘dog-like’ hyenas that are still present at localities such as Lothagam (Werdelin, 2003). At Pliocene localities, hyenas are mainly represented by relatives of the living hyenas. These Pliocene forms had adaptations to a scavenging lifestyle similar to those of living hyenas, but less accentuated. At Laetoli, hyenas are abundant, and include fossil relatives of three of the four living hyenas (Werdelin, unpublished). One of these species is also present at Kanapoi.

Parahyaena Hendey, 1974

There has been some debate regarding the validity of *Parahyaena* as a genus distinct from *Hyaena* (Werdelin and Solounias, 1991; Jenks and Werdelin, 1998). On the one hand, today these are two monospecific sister taxa, and from this perspective, generic distinction may be deemed unnecessary. On the other hand, the split between the two, as inferred from both molecular and paleontological evidence, extends down into the Miocene, and most generic splits among carnivores are of about this age or even younger. From this perspective, generic separation is valid. Here I follow the latter path, as I believe that geological age is the only criterion with which to resolve ranking issues when these become critical. Until now, *Parahyaena* was known from the single extant species *P. brunnea* (Thunberg, 1820), which has a limited distribution and geological age (Jenks and Werdelin, 1998). A single record extends the range of *P. brunnea* into eastern Africa in the middle Pleistocene (Werdelin and Barthelme, 1997). This makes the presence of an ancestral species of *Parahyaena* at Kanapoi highly significant.

Parahyaena howelli sp. nov.

(Figures 2–5)

Hyaena sp. Behrensmeyer, 1976
Pachycrocuta sp. Howell and Petter, 1980

DIAGNOSIS. Hyaenid of large size (larger than *Hyaena hyaena* Linnaeus, 1758). Mandibular ramus robust, premolars moderately developed for bone cracking (weaker than in *Pliocrocuta* Kretzoi, 1938, *Pachycrocuta* Kretzoi, 1938 and *Crocuta* Kaup, 1828). Masseteric fossa clearly subdivided by a ridge into a ventral and dorsal part (unlike *H. hyaena*). Metastyle of P4 clearly longer than paracone (unlike *Ikelohyaena abronia* (Hendey, 1974) and *H. hyaena*). Metacarpals short and robust (unlike all modern hyenas).

HOLOTYPE. KNM-KP 30235, associated partial skeleton (Figs. 2, 3).

ETYMOLOGY. After Dr. F. Clark Howell, leading scholar of African fossil carnivores.

KANAPOI MATERIAL. 10033, complete right mandibular ramus with c–m1 (Fig. 2A, *Hyaena* sp. in Behrensmeyer 1976; *Pachycrocuta* sp. in Howell and Petter 1980); 29249, right mandibular ramus fragment with p4; 29280, proximal fragment of left radius; 29290, right mandibular ramus fragment with p4, distal left radius fragment, right radius shaft fragment; 29293, left distal radius fragment; 29294, right mandibular ramus fragment with p2; 29296, right mandibular ramus fragment with partial alveolus for c, alveolus for p2, roots of p3, anterior root of p4; 29297, left mandibular ramus fragment with roots of p4 and anterior root of m1; 29299, proximal, shaft, and distal fragments of right femur; 29301, left mandibular ramus fragment with p4 and anterior root of m1, separate p3; 29302, left P4; 30229, right femur lacking distal end, proximal right tibia; 30234, associated partial left forelimb with left ulna lacking olecranon, left radius, left humerus lacking proximal articulation, left scapholunar, left magnum, left pisiform, left unciform; 30235, associated partial skeleton including right mandibular ramus with i2 and c–m1 (Fig. 2B), left distal humerus fragment, right proximal and distal humerus fragments, right radius (Figs. 3A–B), right calcaneum, right tibia lacking distal articulation, right ulna lacking distal articulation, fragments of the right and left scapulae, left cuboid, right and left navicular, right scapholunar, left lateral cuneiform, damaged right lateral cuneiform, right unciform, ?right patella, left MC II lacking distal articulation, right MC II lacking proximal articulation, proximal part of right MC III, left and right MC V lacking proximal articulations, right MC I, distal part of right MT II, right MT IV lacking proximal articulation, left and right MT V lacking proximal articulations, proximal, middle and distal phalanges including proximal phalanx of digit 1 of the manus, pisiform, sternebrae, and cervical, thoracic, lumbar, and caudal vertebral fragments; 30272, associated partial skeleton with right mandible fragment with c, damaged p3, roots of p2 and p4, left mandible fragment with roots of p2–p3, right maxilla fragment with C root, P1 alveolus, nearly complete P2, roots of P3, anterior root of P4, left maxilla fragment with alveolus for I3, damaged C, roots of P1–P2, anterior root of P3, right zygomatic, proximal end of right and left scapulae, fragment of distal right humerus shaft, right tibia, proximal, shaft and distal fragments of left tibia, pelvic fragment, left navicular, proximal fragment of left MT V, tuber fragment of left calcaneum, partial distal right femur, proximal and distal fragments of left femur, fragment of left pisiform, proximal end of right MC III, pathological left MT II, distal end of left MT III, right MT III, proximal fragment of right and left MT IV, proximal end of right MT V, proximal phalanx of left manus digit 3, proximal phalanx of right manus digit 4, proximal phalanx of right manus digit 5, middle phalanx of right manus digit 4, middle phalanx of right and left pes digit 4, middle phalanx of right and left pes digit 5, sternebrae, fragments of cervical, thoracic, lumbar, and caudal vertebrae; 30306, left distal femur fragment; 30463, right mandibular ramus fragment with roots of p2–p4; 30482, associated complete left MC III–V (Fig. 4); 30487, proximal part of left MT III; 30495, proximal fragment of MT II; 30534, proximal right MT III; 30536, left p3; 30540, right I3; 30541, right lower canine; 30544, left mandibular ramus fragment with p3 and m1, p2 and p4 crowns separate; 31734, proximal right ulna; 31735, proximal left ulna lacking olecranon; 32538, right m1; 32550, left P3; 32552, mandible fragments with associated left c and p3–m1; 32813, proximal right ulna fragment; 32822, left lower canine; 32865, postcranial fragments including a fragment of a proximal MC II, distal metapodials, a distal humerus fragment, and vertebral fragments.

MEASUREMENTS. See Tables 1 and 2

The following is a composite description of the material. The craniodental material shows limited variability, except in size, but where there is variation, this is noted. There is limited duplication between postcranial elements, which allows for a very limited grasp of variation in the taxon, but does mean that a significant proportion of the skeleton of *Parahyaena howelli* is actually known (Fig. 5). Some comparisons with representative morphologies of extant *Hyaena hyaena* are made.

SKULL AND UPPER DENTITION. The skull is represented only by some very small fragments from KP 30272, which unfortunately are too small and damaged to provide any information about the morphology of the species. This specimen has some very damaged teeth and tooth roots that indicate that the upper canine was slightly larger than the lower, that the P1 was small and single rooted, and that P2 was considerably smaller than P3. All these features are normal in hyenas and the only fact of interest is the presence of P1. The I3 is represented by specimen KP 30540, which is worn, but shows the distinctive derived hyaenid subcaniniform morphology of this tooth. The P3 is also represented by a damaged specimen, KP 32550. This tooth probably had a small anterolingual accessory cusp, though damage in this area makes this somewhat uncertain. The main cusp is high and conical, as is typical of derived hyenas, and the posterior accessory cusp is substantial, though precisely how large cannot be determined due to specimen damage. The tooth is similar to P3 of modern *Hyaena,* but the main cusp is larger and stouter. The upper carnassial is represented by the isolated tooth KP 29302. It is typically hyaenid in morphology, with substantial parastyle and protocone, a large and relatively narrow paracone and a long metastyle. The parastyle is robust with a distinct anterior ridge leading down to an anterior cingulum with a hint of a preparastyle. The protocone is large but low and set in line with the anterior margin of the parastyle. The paracone is tall and trenchant and the metastyle long. There is a lingual cingulum that reaches from the posterior root of the protocone to the posterior quarter of the metastyle.

MANDIBLE AND LOWER DENTITION. The mandible and associated material are known from sixteen specimens, most of which are fragmentary and damaged, but include two nearly complete rami, KP 10033 and KP 30235A (Figs. 2A–B). The mandible increases gradually in depth from anterior to posterior and is deepest just posterior to m1. Posterior to this point, the ventral margin of the mandible rises in a shallow S shape to the angular process. The mandibular condyle is relatively slender in comparison with modern *Hyaena* and consists of two semidistinct areas, a lateral, higher one and a medial, lower one. The latter does not taper medially as is the case in *Hyaena.* The coronoid process is tall and slender compared with that of modern *Hyaena,* and has a distinct backward tilt. The anterior margin of the coronoid process is steeply S shaped. The masseteric fossa is deep and flat. The ventral part (insertion area for the *M. masseter intermedius*) is delimited by a strong ridge and is set distinctly lateral to the more dorsal parts of the masseteric fossa (insertion area for the *M. masseter profundis*). This is in contrast with the situation in *Hyaena,* where the ridge separating these two insertion areas is lower and less distinct and the two areas are located in the same vertical plane. There is a single, large mental foramen situated beneath p2. In KP 10033, the symphysis is broken and all the incisors lost. The lower canine is broken and chipped, but can be seen to have been a relatively robust tooth whose anteroposterior axis is angled relative to the main axis of the ramus. The diastema is of about the same length as in *Hyaena.* The cheek tooth row curves gently to buccal from p2 to p3, then curves gently back from p4 to m1, much as in modern *Hyaena.* Unlike the latter, however, the p2 of KP 10033 is set at an angle to the main axis of the ramus.

The i2 is present only in KP 30235A. It is heavily worn, but is clearly longer (anteroposteriorly) than wide (mesiodistally). The tip is worn flat, though the wear facet is angled from distal (higher) to mesial. On the mesial side, the wear has reached the enamel–dentine juncture. The lingual face is also worn and there is an angle of about 70° between the apical and buccal wear facets. The p2 is the most variable tooth in both size and shape. There is no anterior accessory cusp, but a small swelling at the anterior end of the tooth is present. The main cusp is narrow and conical, with slightly convex anterior and posterior margins. The posterior accessory cusp is low and narrow. The posterior shelf of this tooth is variable in width. In KP 10033, it is narrow in comparison with modern *Hyaena,* which has a small shelf that is not present in this Kanapoi specimen. In KP 30235A and KP 30544, p2 is much broader posteriorly and more similar to the condition in *Hyaena.* In KP 29296, the p2, as judged from the alveolus, must have been noticeably shorter than in the other specimens that preserve traces of this tooth. The p3 has no anterior accessory cusp. Instead, the anterior margin of the main cusp is formed into a low crest that reaches the anterior end of the tooth. The anterior and posterior margins of the robust, conical main cusp are slightly convex. The posterior accessory cusp is low and round and set centrally in a posterior cingulum shelf. The tooth is variable in size and shape, though not to the extent seen in p2. KP 29301 has a p3 that is nearly identical to that of KP 10033,

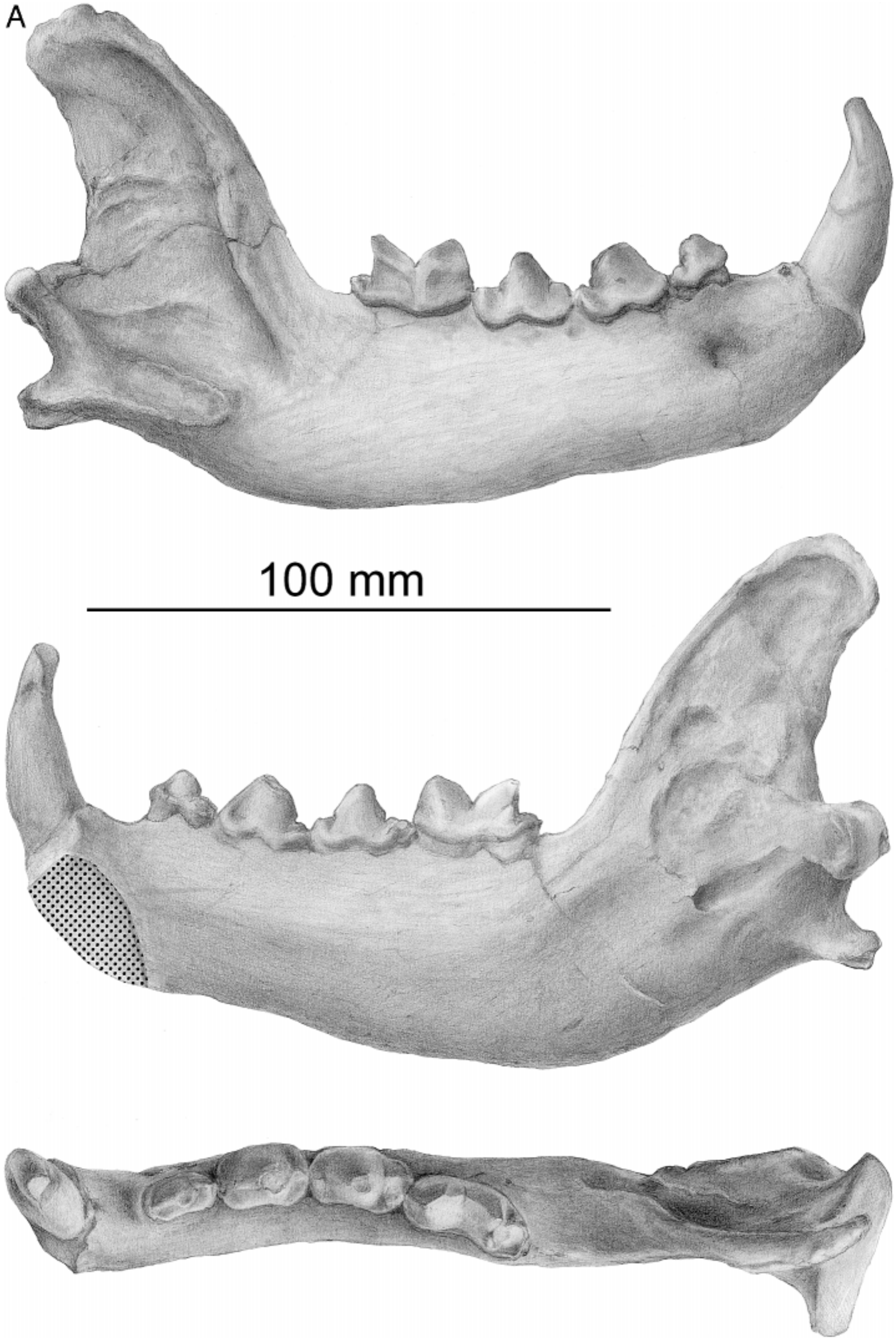

Figure 2 **A,** *Parahyaena howelli,* KP 10033, right mandibular ramus in (top to bottom) buccal, lingual, and occlusal view; **B,** *Parahyaena howelli,* KP 30235A, right mandibular ramus in (top to bottom) lingual, buccal, and occlusal view

whereas in KP 30235A and KP 30544, the p3 is narrower and has a more distinct waist. KP 30536 and KP 32552 are intermediate in morphology. The tooth is broadly similar to p3 in *Hyaena* except for the absence of an anterior accessory cusp. The p4 has a small, round anterior accessory cusp appressed to a narrow, conical main cusp with more or less straight anterior and posterior margins. The posterior accessory cusp is relatively high and trenchant. The posterolingual part of p4 has been dam-

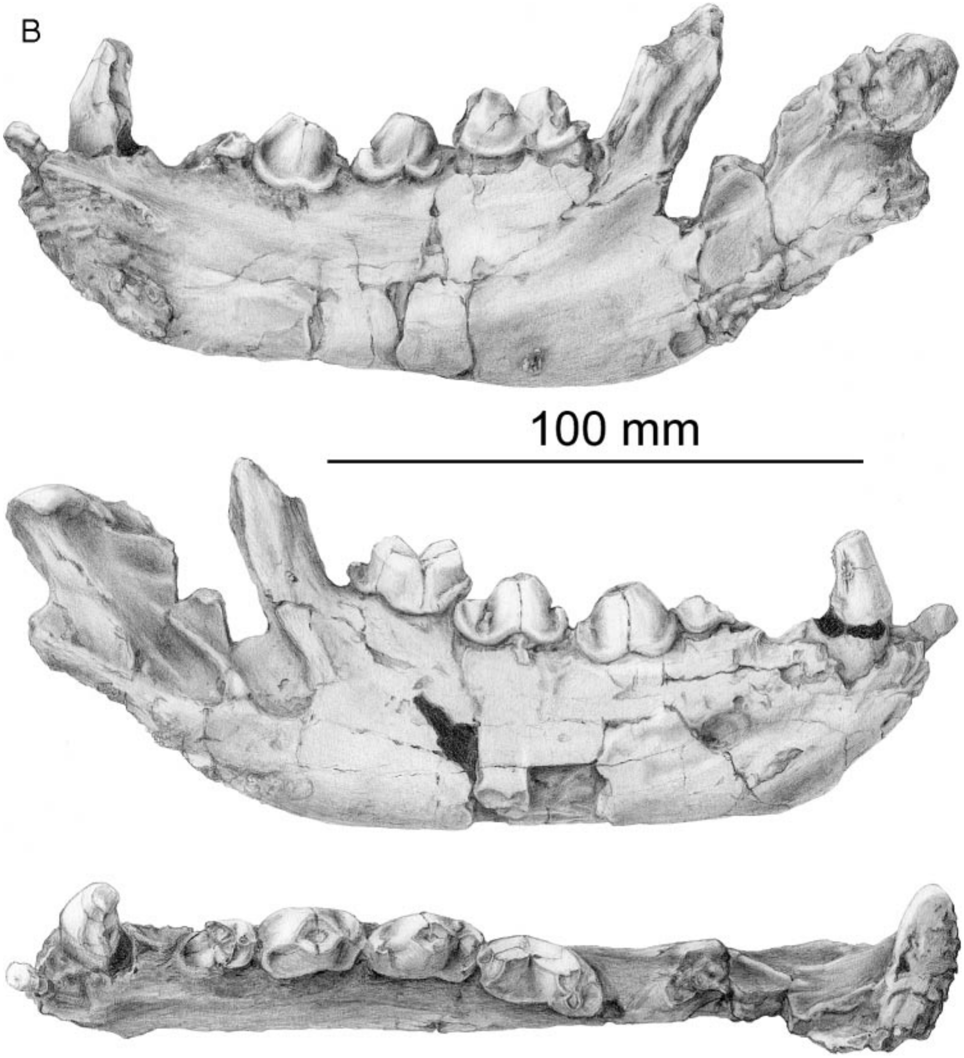

Figure 2 Continued

aged and it is not possible to determine the width of the posterior part of the tooth. The lower carnassial is long and relatively low. The paraconid is slightly longer and wider than the protoconid. The metaconid is very small but is distinctly developed and the talonid has two cusps, presumably the hypoconid and entoconid. Compared with modern *Hyaena,* the tooth is relatively much longer, the metaconid smaller, and the talonid relatively shorter.

FORELIMB. The humerus is known from KP 30235 (proximal and distal pieces) and KP 30234 (shaft and distal articulation). The proximal fragment is too worn for detailed comparisons with *Hyaena,* but is larger and appears relatively narrower. The distal articulation is transversely broader than in modern *Hyaena,* but is relatively more slender anteroposteriorly. There is a large supratrochlear foramen present in KP 30235.

The radius is known from KP 30235 (Figs. 3A–B) and KP 29280. It is in general very similar to that of *Hyaena,* but is shorter for the same robusticity. The grooves for the *extensor digitis communis, extensor carpi radialis,* and *abductor pollicis longus* are all more deeply incised than in *Hyaena.*

The ulna is known from several fragmentary specimens, KP 30234, KP 30235, KP 31734, KP 31735, and KP 32813. The first two are the most complete and indicate that the ulna of this taxon was slightly shorter but more robust than that of *Hyaena.* The shaft is more rounded than in *Hyaena,* the triceps groove is wider, the ridge on the cranial surface of the olecranon is narrower, the attachment area for the *flexor carpi ulnaris* is less distinct, and the pit beneath the radial notch is shallower. In addition, the rugosity for the articulation with the radius begins more proximally on the

Figure 3 *Parahyaena howelli,* KP 30234, right radius in **A,** anterior and **B,** posterior view

shaft, while the groove for the *abductor pollicis longus* is much more distinct than in *Hyaena.*

Several of the carpals are known from different specimens. The scapholunar is known in specimens KP 30234 and KP 30235AC. It is slightly larger and more slender anteroposteriorly than that of modern *H. hyaena.* Specimen KP 30235AC is broken on the medial side, but in KP 30234, it can be seen that the articular face for the radius extends down onto the medial rim, while in modern *H. hyaena,* there is a much more distinct ridge limiting the radial articulation to the dorsal side of the bone. This may indicate greater mobility of this articulation in the fossil form. In addition, the sulcus for the *flexor carpi radialis* tendon is deeper and bounded medioventrally by a more prominent ridge than in modern *H. hyaena.* The magnum is known in KP 30234. It is shorter and wider than that of modern *H. hyaena* but is morphologically very similar in all other respects. The unciform is also known from KP 30234. It is more robust than that of modern *H. hyaena* and has a more open articular face for MC III. The pisiform is known from KP 30234. It is larger than that of modern *H. hyaena,* but aside from size is practically indistinguishable from it.

All the metacarpals except MC II are known from complete specimens. MC I, known from KP

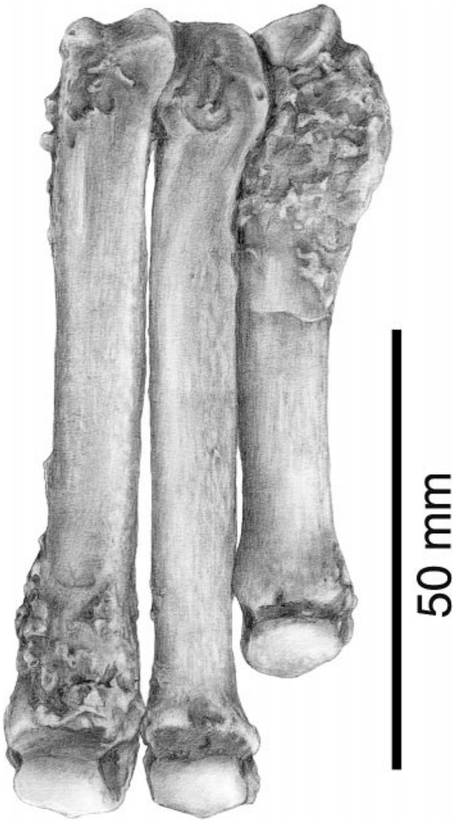

Figure 4 *Parahyaena howelli,* KP 30482, associated left MC III–V in dorsal view. Scale = 50 mm

30235P, is a substantial element associated with at least one phalanx. This is corroborated by KP 39235V, which is tentatively identified as the proximal phalanx of the same digit. This phalanx bears a large articular surface for an ungual phalanx, which has not been identified in the material. It is far larger than that of any extant hyaenid, though relatively smaller than its counterpart in *Ikelohyaena abronia* Hendey, 1974, from Langebaanweg, a species that is otherwise smaller than the Kanapoi form. The second metacarpal is known from a distal and a proximal fragment, KP 30235AH and AO, respectively. This metacarpal is more robust than MC II in modern *H. hyaena.* Metacarpals III to V are associated in specimen KP 30482 (Fig. 4) and MC III is in addition known in KP 30235AG and KP 30235BH and in KP 30272. The third metacarpal has larger proximal and distal articular surfaces than MC III in modern *H. hyaena,* while the shaft is more robust but markedly shorter than in the extant species. The plantar side of the proximal articular surface is narrower relative to the dorsal side than in the modern species. The fourth metacarpal is, like the third, shorter and more robust than that of modern *H. hyaena.* The two species are similar in their MC IV morphology, but the proximal articulation in KP 30482 is somewhat more triangular in shape, with a broader dorsal and narrower plantar side than in the modern form. The fifth metacarpal is also more robust and shorter than that of modern *H. hyaena,* the difference being more accentuated in this element. The proximal articular surface with MC IV is set less obliquely and more directly anteroposteriorly than in modern *H. hyaena* and is also very wide compared with the condition in the modern species.

HINDLIMB. The femur is represented by various fragments from specimen KP 30272, including a partial distal femur KP 30272N, proximal fragments of specimen KP 30229, distal fragments, specimen KP 30306, and proximal, shaft and distal fragments, KP 29299. These fragments suggest a femur that is somewhat larger and more robust than the corresponding element in modern *H. hyaena,* but otherwise do not show any distinguishing features of note.

The tibia is known from fragments from the partial skeletons KP 30235D and KP 30272P, Q, as well as from KP 30229. In general, the tibia is not a very diagnostic bone in Hyaenidae and this is true in the present case as well, the fossil specimens only being distinguished from modern *H. hyaena* by their greater size and by the slightly greater development of the medial malleolus of KP 30272Q.

The navicular is known from KP 30235AE and AD, and KP 30272F. This bone is generally similar to that of modern *H. hyaena,* but is slightly larger. It differs in that the plantar process is wider than high, the reverse of the condition in *H. hyaena.* The process for the separation between the articulation with the cuboid and the plantar side of the bone is less prominent than in *H. hyaena.*

The lateral cuneiform is known only from KP 30235BJ and BP. It is larger than the corresponding bone in modern *H. hyaena,* apparently relatively more so than other tarsals and carpals reported here. The proximal articular surface of the fossil is more deeply indented laterally and medially than in *H. hyaena* and, in addition, the distal articular surface (for MT III) is concave in the fossil rather than slightly convex as in *H. hyaena.*

The cuboid is known from KP 30235W. It is the tarsal that differs most from the corresponding element in modern *H. hyaena.* The medial side of the proximal articular surface of the fossil has a medial extension that probably buttressed the medial part of the sulcus for the *M. peritoneus longus* tendon. This sulcus is shallow and nondescript in modern *H. hyaena,* deep and well developed in KP 30235W. The cuboid of *Crocuta crocuta* (Erxleben, 1777), on the other hand, is short and square with a deep, narrow sulcus.

The second metatarsal is known from KP 30495, 30235AM, and 30272AB. The two former are proximal ends that are more robust than MT II in modern *H. hyaena* but otherwise too worn for

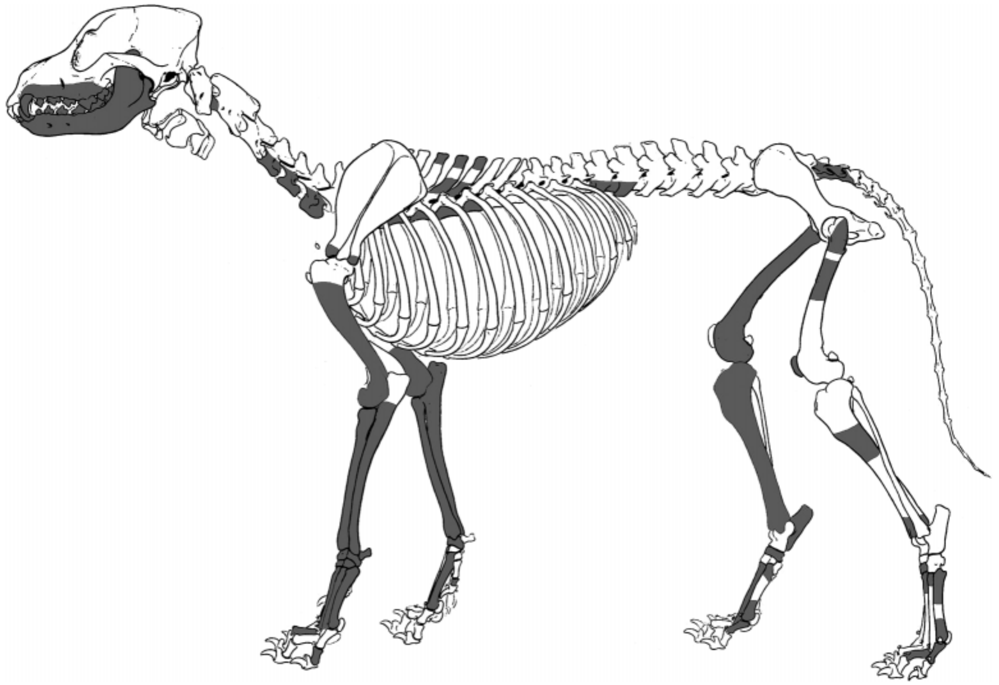

Figure 5 *Parahyaena howelli,* known skeletal parts of *P. howelli* (gray) superimposed on a skeleton of a dog; skeleton adapted from Evans (1993)

meaningful comparisons to be made. The third specimen, KP 30272, is pathological in that the bone appears to have been broken in life and subsequently healed. The distal end of this bone is composed of an amorphous mass of secondary bone suggestive of healing.

The third metatarsal is known from specimens KP 30272U and KP 30272AO, KP 30534, and KP 30487. These specimens are more robust than the corresponding element in modern *H. hyaena,* but are otherwise similar except for the proximodorsal articular surface being concave rather than flat to convex.

The fourth metatarsal is known from KP 30235AF and KP 30272T and AC. It differs from that of *H. hyaena* only in its greater size and in the less expanded proximopalmar eminence.

The fifth metatarsal is known from KP 30235AK and AL and KP 30272AA and KP 30272AP. In this case, the greater size is the only clear difference from extant striped hyaena.

DISCUSSION. KP 10033 was recovered by the American expeditions. It was referred to *Hyaena* sp. by Behrensmeyer (1976) and to *Pachycrocuta* sp. by Howell and Petter (1980). The referral of this species to *Parahyaena* rests chiefly on the length of the metastyle of P4. This is only known from a single specimen, KP 29302, but can also be inferred from the length of the m1 trigonid in relation to p4 and m1 talonid length. The length of the P4 metastyle is one feature that clearly distinguishes all extant hyena species. *Hyaena hyaena* has a short P4 metastyle, of about the length of the paracone or slightly shorter. In *C. crocuta,* the metastyle of P4 is exceptionally long and straight. In *Parahyaena brunnea,* the metastyle of P4 is longer than that of *H. hyaena* but shorter than that of *C. crocuta.* In the present case, the P4 metastyle has the relative length of that of *P. brunnea.* This contrasts with the condition in *Ikelohyaena abronia,* a possible ancestor of *H. hyaena* (Hendey, 1978a; Werdelin and Solounias, 1991), in which the P4 metastyle is short, as in its putative descendant. No other features contradict assignment of the Kanapoi hyena to *Parahyaena,* and rather than posit the existence of a previously unknown hyaenid lineage, I prefer to suggest a link to the living brown hyena. This represents the first direct indication of the ancestry of the brown hyena, as all other known fossil *Parahyaena* fit comfortably within the extant species (e.g., Hendey, 1974).

Family Felidae

Felids are common elements in the fossil faunas of eastern Africa. Both Machairodontinae and Felinae are present throughout the Plio–Pleistocene, but up to about 1.5 Ma, the former are by far the more common in the fossil record.

Table 1 Dental measurements of *Parahyaena howelli* **n. sp.; measurement parameters as in Werdelin and Solounias (1991)**

	KP10033	KP30235	KP30541	KP29290	KP29301	KP29249	KP30536	KP32538	KP32822	KP32552	KP32550	KP29302
MLc	12.9		14.0						e15.5	16.0		
Wc	10.4	10.9	10.0						e11.0			
MLp2	13.7											
Wp2	7.9	8.6										
MLp3	18.1	20.0			19.0		19.1			20.3		
Wp3	11.6	11.7			11.7		11.9			a11.9		
MLp4	20.2	21.8			20.4					21.3		
Wp4	11.4	11.7		11.8	11.3	10.9				12.1		
MLpp4	10.0	12.4								11.4		
MLm1	24.3	a25.1								24.5		
Wm1	10.5	11.4						11.8		11.0		
MLtm1	19.9	a20.9						a21.3		19.8		
MLP3											a20.4	
MLP4												34.1
WaP4												18.8
WblP4												9.9
MLpP4												12.0
MLmP4												13.6

a = approximate, e = estimated

Table 2 Postcranial measurements of *Parahyaena howelli* **n. sp.**

	KP30235	KP30234	KP29280	KP30482	KP30534	KP29293	KP32865
Humerus DistW	46.6	46.1					
Radius L	215.5						
Radius ProxW max	22.3	a21.4					
Radius ProxW min	15.7	16.0					
Radius DistW transv	31.9					32.4	
Radius DistW a–p	20.9					20.7	
MC II ProxW transv					10.6		11.8
MC II ProxW a–p					14.8		14.5
MC III L				91.5			
MC III ProxW transv	13.5			12.5			
MC III ProxW a–p	14.8			15.2			
MC III DistW transv				a14.3			
MC III distW a–p				11.5			
MC IV L				89.3			
MC IV ProxW transv				12.2			
MC IV ProxW a–p				14.6			
MC IV DistW transv				13.6			
MC IV DistW a–p				12.5			
MC V L				75.9			
MC V ProxW transv				18.6 (14.0)			
MC V ProxW a–p				15.6 (13.9)			
MC V DistW transv				15.8 (12.9)			13.1
MC V DistW a–p				11.9			12.3

	KP30272	KP29299	KP30229	KP30235
Femur HeadW		24.3	24.7	
Femur ProxW		51.4	a53.3	
Femur DistW	41.4	a42.4		
Tibia ProxW			44.0	43.7
Tibia DistW	23.9			
Calcaneus Head W transv				14.4
Calcaneus HeadW a–p				20.5
Calcaneus tuber Wmax				20.4
Calcaneus tuber Wmin				11.0
Calcaneus SustW				24.3

	KP30495	KP30487	KP30272
MT II ProxW transv	a9.9		
MT II ProxW a–p	a12.5		
MT III ProxW transv		11.5	10.8
MT III ProxW a–p		17.6	18.3
MT IV ProxW transv			9.8
MT IV ProxW a–p			16.5
MT V ProxW transv			8.2
MT V ProxW a–p			13.1

Dinofelis Zdansky, 1924

Species of the genus *Dinofelis* are among the most common Felidae in the fossil record of eastern Africa. The earliest record there and possibly the earliest anywhere is from Lothagam, where material referred to the genus is known from all members (Werdelin, 2003). The genus is subsequently present at most Plio–Pleistocene sites in eastern Africa until its last occurrence at Kanam East (ca. 1.0 Ma; Werdelin and Lewis, 2001).

Dinofelis petteri Werdelin and Lewis, 2001

(Figure 6)

KANAPOI MATERIAL. 30397, complete right mandibular ramus with c–m1 (Fig. 6); 30542, distal left ulna; ?30429, P4 metastyle.

MEASUREMENTS. KP 30397, Lc = 13.9, Wc = 9.7, Lp3 = 13.1, Wp3 = 7.3, Lp4 = 20.6, Wp4 = 9.7, Lm1 = 23.2, Wm1 = 10.6. Measurement parameters defined in Werdelin and Solounias

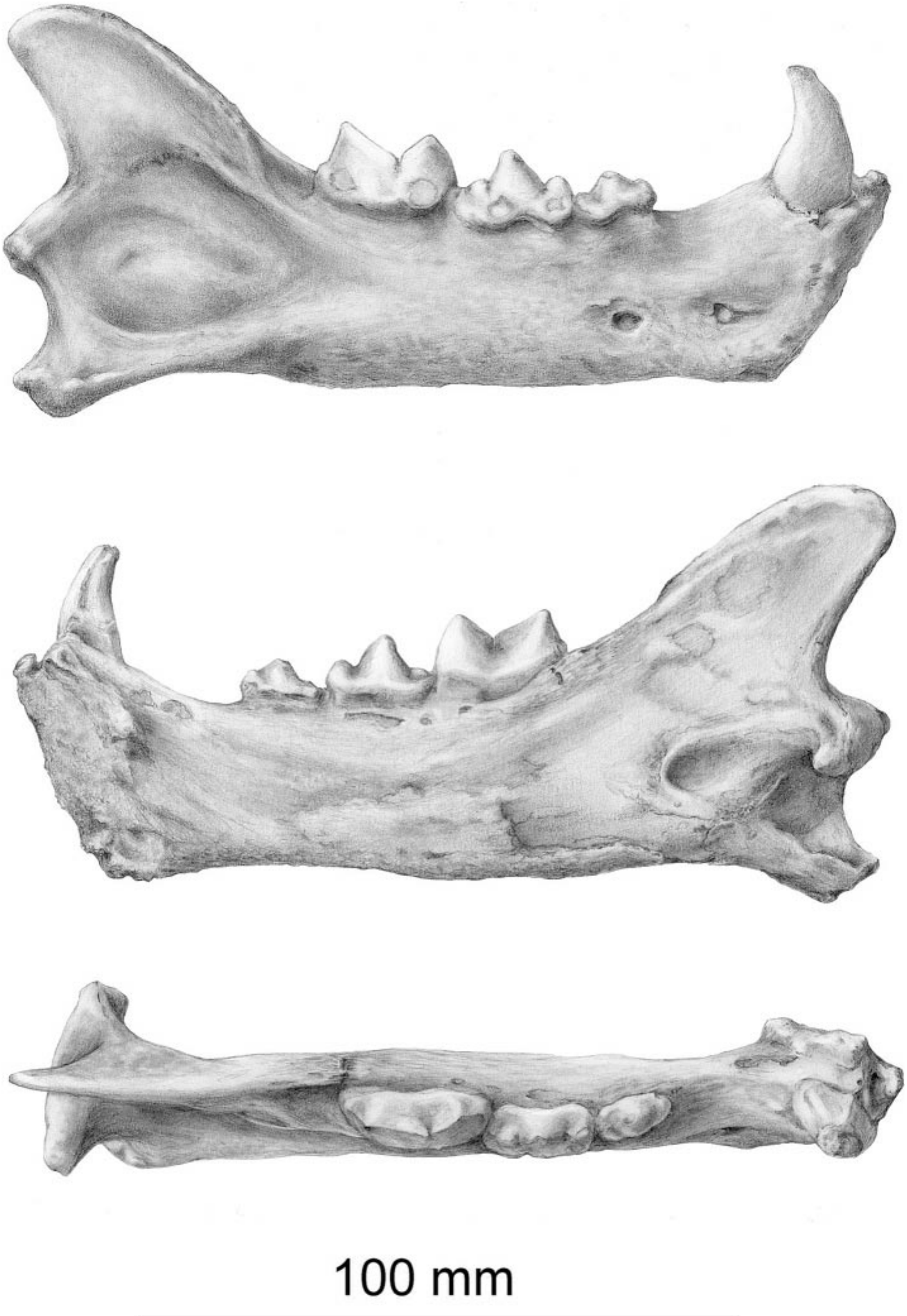

Figure 6 *Dinofelis petteri*, KP 30397, right mandibular ramus in (top to bottom) buccal, lingual, and occlusal view

(1991). The horizontal ramus is low, but broad, with a noticeable thickening of the corpus. The depth is about the same throughout. The symphysis is deep and short and nearly vertically oriented, producing a small anteromedial chin. There are two mental foramina, one below the diastema between the canine and p3 and one beneath the anterior root of p3. Both are set low on the ramus. The masseteric fossa is deep and the masseteric foramen large, while the coronoid process is relatively short anteroposteriorly. The condyle is thickest medially and tapers gradually toward the lateral end. The angular process is robust and angled ventrally relative to the horizontal ramus.

The space for the incisors is very narrow, suggesting that they were either staggered or very small. The lower canine is short and robust and angled outward with respect to both the anteroposterior axis of the ramus and the sagittal plane. The diastema is long. The p3 has a small anterior accessory cusp, a low, conical main cusp, and a posterior basin that forms the widest part of the tooth but lacks a posterior accessory cusp. The p4 is long and slender. The anterior accessory cusp is well developed and set far anteriorly, well away from the main cusp. The main cusp is triangular with straight anterior and posterior margins. The posterior accessory cusp is similar in size to the anterior but set closer to the main cusp. There is a small posterior cingulum cusp and a low lingual cingulum crest, making the posterior basin the widest part of the tooth. The lower carnassial is typically felid, with a broad paraconid and narrower and somewhat longer protoconid. There is a minute, posteriorly located talonid. The m1 is set in a groove at the posterior end of the horizontal ramus. This groove is bounded laterally by the masseteric fossa wall and medially by the root of the ascending ramus.

The tip of the anconeal process of the ulna is broken and the specimen is somewhat eroded. It is a relatively small, gracile bone compared with later, better known *Dinofelis* (see Werdelin and Lewis, 2001 for a discussion).

DISCUSSION. This and other *Dinofelis* material from Africa and other regions is described and extensively discussed elsewhere (Werdelin and Lewis, 2001). The Kanapoi material is referred to the species *D. petteri,* which is also known from a number of other sites (Allia Bay, Laetoli, Hadar Sidi Hakoma, and Denen Dora Members, Omo Shungura Members B–F, Koobi Fora Tulu Bor Member, West Turkana Lomekwi Member) in eastern Africa. This gives the species a temporal range of ca. 4.2 Ma (Kanapoi) to 2.3 Ma (Shungura Member E/F).

Homotherium Fabrini, 1890

Material that can be referred to *Homotherium* is relatively ubiquitous at eastern African Plio–Pleistocene sites. Unfortunately, much of this material is fragmentary or undescribed. Therefore, the taxonomy of eastern African *Homotherium* is confused. Petter and Howell (1988) described a skull from Hadar as *Homotherium hadarensis,* noting its differences from Eurasian *Homotherium.* On the other hand, Harris et al. (1988) described a skull from West Turkana, tentatively affiliating it with *Homotherium problematicum* (Collings et al., 1976). The latter comparison cannot be maintained, but neither does the West Turkana skull seem to belong to *H. hadarensis.* African *Homotherium* requires renewed investigation for the resolution of these problems.

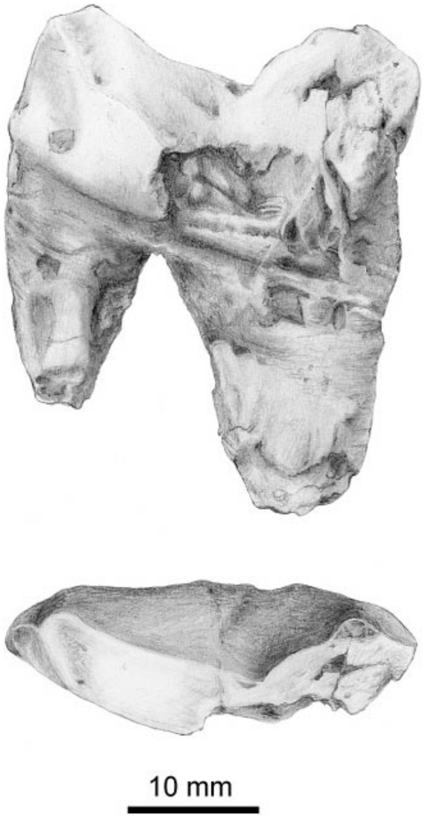

Figure 7 *Homotherium* sp., KP 30420, right m1 in (top) buccal and (bottom) occlusal view

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Homotherium sp.

(Figure 7)

KANAPOI MATERIAL. 30420, right m1 (Fig. 7); 32558, complete right MC IV; 32820, complete proximal phalanx; 32882, proximal metatarsal fragment.

The lower carnassial is very long and slender. The paraconid is slightly broader than the protoconid, but the latter is the longer of the two cusps. There is no metaconid and no talonid. The shaft of MC IV is relatively straight and quite rounded in cross-section, widest just below proximal articulation and gradually tapering distally. The distal articulation is about as tall as it is wide. The proximal phalanx is large and robust. The shaft is gently arched. The proximal articulation is broad and low, while the distal articulation is more nearly equal in height and width, though the width is still somewhat greater. Rugose surfaces are prominent on the medial and lateral sides of the shaft.

DISCUSSION. All of this material is clearly felid and is too large to represent any taxon other than *Homotherium.* The m1 matches the lower carnassial of most other *Homotherium* in size and proportions, though it is distinctly smaller than m1 from a *Homotherium* mandible from Koobi Fora (KBS Member), as well as that of *H. problematicum* from Makapansgat. However, none of the Kanapoi material can be considered diagnostic among species of *Homotherium* and the material must be left as indeterminate species for the time being. The Kanapoi material represents the hitherto oldest described material of *Homotherium* in eastern Africa.

Felis Linnaeus, 1758

Fossils of the genus *Felis* are very rare in the fossil record of eastern Africa. In fact, aside from the Kanapoi record, only a single specimen from the Denen Dora Member of the Hadar Formation can be unequivocally referred to *Felis sensu stricto* (personal observations).

Felis sp.

KANAPOI MATERIAL. 30546, fragments of P4 of one or two individuals.

This material comes from a small feline, smaller than "*Felis* small species" from Laetoli (Barry, 1987). It is the size of the extant *F. lybica* Forster, 1780. The main cusp is taller and shorter anteroposteriorly than in the Laetoli specimen.

DISCUSSION. Given the fragmentary nature of the material, as well as the almost complete lack of knowledge of fossil African *Felis* at the present time, it is inadvisable to put a specific name to this material.

Family Herpestidae

Apart from the notable exceptions of Laetoli and Olduvai, sites that have been excavated for micromammals, herpestids are rare in the fossil record of eastern Africa. Because of the lack of screen-washed localities, it is not at present possible to establish whether this is a sampling artifact, whether it reflects a biased sample of localities vis-à-vis environment, or whether it is a real phenomenon.

Helogale Gray, 1861

Dwarf mongooses are among the more common herpestids in the Plio–Pleistocene of eastern Africa, with several species described from Laetoli and the Shungura Formation (Wesselman, 1984; Petter, 1987).

Helogale sp.

KANAPOI MATERIAL. 32826, fragments of a right mandibular ramus with broken p4, damaged m1, roots of m2; 31034, lower canine.

This material belongs to a very small carnivore species. The horizontal ramus is slender but relatively deep. In the carnassial, the paraconid is by far the largest and tallest cusp, making up about half of the trigonid in occlusal view. The protoconid is small and set buccally. The carnassial notch is relatively shallow. The metaconid is set directly behind the paraconid and lingual to the protoconid. It is separated from both by shallow valleys. The talonid is low and short. The hypoconid is prominent, the entoconid less so. The m2 is single rooted, while the p4 is too damaged to provide any useful morphological information.

DISCUSSION. To the extent that comparisons can be made, this material strongly resembles *Helogale* species. It is a little larger than *H. palaeogracilis* (Dietrich, 1942) from Laetoli by the same amount that that species is larger than the extant *H. hirtula* (Thomas, 1904). The Kanapoi material clearly is not adequate for specific identification, and I prefer to leave it as *Helogale* sp. herein.

Family Viverridae

Viverrids are not uncommon in the Plio–Pleistocene of eastern Africa, but very little of the material has as yet been published. However, most of the material pertains to species larger than any living viverrid. Such species are found in three lineages, *Viverra* Linnaeus, 1758, with *V. leakeyi* Petter, 1963, known from a number of localities, *Pseudocivetta,* with the single species *P. ingens* Petter, 1973, of uncertain affinities, and a third species from Koobi Fora that may be related to *Civettictis* (Petter, 1963, 1973; Hunt, 1996). Smaller viverrids are less common, and almost none of the material has been studied.

Genetta Cuvier, 1816

Genetta sp. nov.

(Figure 8)

Material that can be referred to *Genetta* is known from a number of localities in the Plio–Pleistocene of eastern Africa. Kanapoi is the oldest of these, though material referred to cf. *Genetta* (two species) is known from Lothagam (Werdelin, 2003). Younger localities with material of *Genetta* sp. include Laetoli and the Shungura Formation, members B and C. The first record of the extant *G. genetta* (Linnaeus) is from the Upper Burgi Member of the Koobi Fora Formation (personal observations).

KANAPOI MATERIAL. 32565, left maxilla fragment with posterior half of P3 and complete P4–M1; 32815, left mandibular ramus fragment with m1 and roots of p4 and m2 (Fig. 8); 30222, left lower canine.

The maxilla fragment represents a small carnivore species. The P3 is damaged anteriorly. It has a small but relatively tall posterior accessory cusp. The upper carnassial is elongated, with a small but sharp parastyle. The protocone is large and reaches further anteriorly than the parastyle. It is separated from the paracone by a deep valley. The paracone is large but short and pyramidal in shape. The metastyle is long and low, longer than the paracone. The M1 is broad but short and set at about 60° to P4. The parastyle wing is large and well developed,

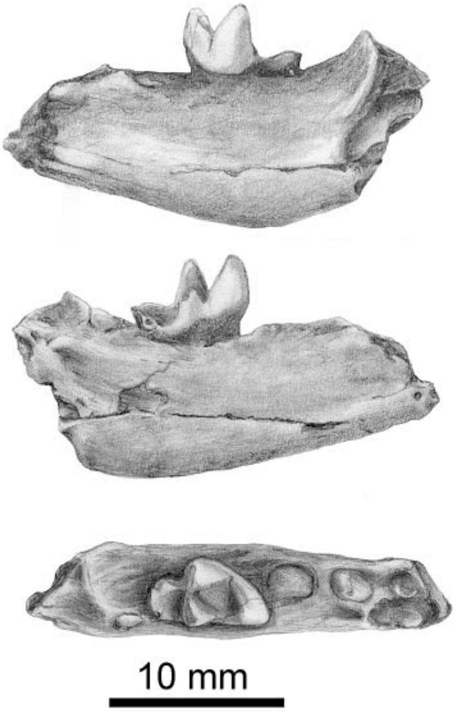

Figure 8 *Genetta* n. sp., KP 32815, left mandibular ramus fragment in (top to bottom) buccal, lingual, and occlusal view

while the metastyle wing has been reduced. Both the paracone and the metacone are present, with the paracone being the larger of the two. The tooth tapers gradually in length to the protocone, which is the largest single cusp of the three cusps on M1. There is a deep basin between the paracone–metacone and protocone.

The horizontal ramus of the mandible is fairly thick and deep, becoming deeper but thinner at the level of the ascending ramus. The masseteric fossa reaches to the posterior end of m1. The lower carnassial has a trigonid with tall cusps and a short, narrow talonid. In occlusal view, the paraconid is the largest cusp, but the protoconid is taller. The long axis of the paraconid is set at nearly right angles to the main axis of the tooth. The carnassial notch is deep, while the notch separating the paraconid from the metaconid is shallower but wider. The paraconid–protoconid shearing blade is set at about 45° to the main axis of the ramus. The protoconid is set buccally, overhanging the ramus to some extent. The metaconid is set directly posterior to the paraconid and lingual to the posterior end of the protoconid. It is separated from the protoconid by a shallow transverse valley. The talonid is very low and short compared to the trigonid. There are two distinct cusps, which can be homologized with the entoconid and hypoconid. The m2 was small and single rooted.

The lower canine KP 30222 is small and recurved. The root is robust and relatively straight, though broken off part way down. The crown shows no accessory cusps or grooves.

DISCUSSION. The morphology of the teeth readily identify these specimens as belonging to the genus *Genetta*. They are similar in size and most features to the extant *G. genetta,* but there are differences that indicate that the Kanapoi material represents a separate species. These differences include the less reduced protocone, broader P4 blade, and less reduced M1. These are all features in which the extant *G. genetta* is more derived than the Kanapoi form.

Carnivora Family Indet.

The following specimens have not been identified to family, mainly because of their incomplete nature. In view of the relative abundance of the species in the identified material, it seems likely that most, if not all, the material of “medium species” should probably be referred to *Parahyaena* sp. nov. 29289, distal metapodial fragment, medium species; 32827, proximal phalanx, medium species; 32517, distal fragment of left? MC V?, small species (may not be carnivore); 32549, proximal metapodial fragment (may not be carnivore); 31738, distal metapodial fragment, medium species; 32808, proximal phalanx, medium species; 32569, fragment of anterior premolar, possibly P1, medium species; 32540, left lower canine, small species (possibly mustelid); 478, fragment of astragalus, large species (Machairodontinae indet. in Behrensmeyer 1976); 30478, vertebral fragments and distal metapodial fragment, medium species; 30494, vertebral centrum; 32883, vertebral fragments including dens of axis, medium species; 30432, distal right humerus condyle; 29291, fragment of distal left femur; 30469, fragment of proximal left femur; 29298, right upper canine.

SUMMARY

The Kanapoi carnivore fauna, with its eight species in as many genera, representing five families, is a substantial addition to the early Pliocene record of Carnivora in Africa. It shares a number of genera and species with other African early–middle Pliocene localities, such as Langebaanweg and Laetoli, but overall has a unique mixture of species. Similarities with Langebaanweg, which is somewhat older and relatively distant, are at the generic level (*Enhydriodon, Dinofelis, Homotherium*), while similarities with Laetoli, which is closer both in age and geography, lie at the species level (*Parahyaena howelli, D. petteri*). The small number of taxa from the Apak Member at Lothagam makes comparisons with that site difficult.

On the other hand, differences between Langebaanweg and Kanapoi show that the former still includes Miocene relicts (taxa such as *Hyaenictis* Gaudrey, 1861, *Plesiogulo* Zdansky, 1924, and

Machairodus Kaup, 1833), while the latter is more typically Pliocene and lacks these Miocene forms.

The Nawata Formation at Lothagam includes a number of forms whose affinities lie outside Africa (mostly in western Eurasia, but also on the Indian subcontinent). The Kanapoi fauna, on the other hand, includes only forms whose immediate forebears can be found in Africa. Thus, the Kanapoi fauna represents the currently best-known evidence for the first post-Miocene radiation of endemic African Carnivora.

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