

# Plio-Pleistocene Carnivora of eastern Africa: species richness and turnover patterns

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This paper presents an up-to-date and detailed overview of the Plio-Pleistocene fossil record of Carnivora in eastern Africa. Major events in the carnivoran lineages present in the region are discussed and stratigraphic ranges of all species-level taxa are provided. The compiled data are used for quantitative analyses of species richness and turnover. Sampling is considered to be adequate for the interval 3.6–1.5 Mya, and poorer in the half-million-year time slices before and after this interval. Species richness peaks around 3.6–3.0 Mya and declines gradually from that time until the end of the time period analysed. Calculation of origination and extinction rates indicate that there are two peaks of origination: at 3.9–3.3 Mya (although the earlier half of this interval is biased through poor sampling) and at 2.1–1.8 Mya. The origination rate is zero in the interval 3.0–2.4 Mya. The extinction rate peaks at around 3.0 Mya after which it falls slightly, remaining nearly constant until 1.8 Mya, after which it increases considerably. The data support the hypothesis that the modern carnivoran guild of eastern Africa originated relatively recently, mostly within the last million years. There is no support in these data for a turnover pulse in Carnivora between 3 and 2 Mya. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 144, 121–144.

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## INTRODUCTION

The Carnivora of the Plio-Pleistocene deposits of eastern Africa have been comparatively neglected in the literature relative to the Bovidae, Suidae and (not least) Hominidae. A major reason for this may be the perceived irrelevance of the Carnivora for stratigraphic (cf. Suidae) and palaeoecological (cf. Bovidae) analysis of the geological and biological contexts of our early ancestors. However, considerable archeological and anthropological work has demonstrated the importance of carnivorans to our understanding of those ancestors' place in the eastern African ecosystem (e.g. Blumenschine, 1987; Bunn & Ezzo, 1993; Selvaggio, 1994; Brantingham, 1998). As a result, there is increased interest in understanding which carnivoran species were present when and in which localities and, in a broader perspective, which specific adaptations these species had at any particular time or place. Our

aim in this paper is to provide an overview of current knowledge of Plio-Pleistocene Carnivora from eastern Africa. Most of what is presented here is based on the first-hand study of the fossils that form the basis for our ongoing revision of these groups, supplemented by a few additions to the listings from the published literature. The material studied is extensive, consisting of hundreds of fossils ranging from complete or near complete skeletons to small scraps of bone. Table 1 provides a list of localities studied.

A few compilations of carnivoran taxa in the Plio-Pleistocene of eastern Africa have appeared over the past decades, but only one large-scale study (Petter & Howell, 1985) was based on first-hand study of the specimens. In this work, Petter and Howell compiled lists of the genera and species within each family of Carnivora (both large and small) known from the later Pliocene; this did not constitute a stratigraphic scheme or table of the eastern African Carnivora. They indicated at which localities members of each taxon known to them had been found, discussed the palaeo-

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**Table 1.** Carnivora localities studied in the present review. Their age data are taken from published sources (Drake & Curtis, 1987; Potts, 1988; Feibel *et al.*, 1989; Walter & Aronson, 1993; Walter, 1994; Leakey *et al.*, 1998; Ditchfield *et al.*, 1999; McDougall & Feibel, 1999; Ward *et al.*, 1999), as well as personal communications from M. G. Leakey, C. S. Feibel, R. Potts and K. E. Reed. Additional localities where data on Carnivora were obtained from the published literature include Aramis (WoldeGabriel *et al.*, 1994), Konso-Gardula (Asfaw *et al.* 1992), and Daka Mb., Bouri Fm. (Gilbert, 2003), all in Ethiopia, and Nyaburu and Nkondo (Petter *et al.*, 1991), both in Uganda

Country	Locality	Member (Mb.)	Age
Kenya	Lothagam	Kaiyumung	c. 3–2.5 Mya
	Kanapoi		4.23–4.07 Mya
	Allia Bay		c. 3.9–3.7 Mya
	South Turkwel		3.5–3.2 Mya
	Koobi Fora*	Lonyumun	4.35–4.1 Mya
		Lokochot	3.5–3.36
		Tulu Bor	3.36–2.68
		Upper Burgi	2.0–1.88 Mya
		KBS	1.88–1.64 Mya
		Okote	1.64–1.39 Mya
		Chari	1.39–0.74 Mya
	West Turkana	Kataboi	4.1–3.36 Mya
		Lomekwi	3.36–2.52 Mya
		Lokalalei	2.52–2.35 Mya
		Kalochoro	2.35–1.88 Mya
		Kaitio	1.88–1.6 Mya
		Natoo	1.6–1.33 Mya
		Nariokotome	1.33–0.7 Mya
			c. 1.8–1.6 Mya
	Nakoret		
	Eshoa Kakurongori	c. 3 Mya	
	Kosia		c. 4 Mya
	Olorgesailie		990 ka
	Lainyamok		392–330 ka
	Kanam East		c. 1–0.9 Mya
Ethiopia	Hadar	Sidi Hakoma	3.40–3.28 Mya
		Denen Dora	3.22–3.18 Mya
		Kada Hadar	3.18–2.92 Mya
		Lip	2.92–2.33 Mya
		Pinnacle	c. 2–1.8 Mya
	Omo	Usno	3.07–3.0 Mya
		Shungura A	3.4–3.36 Mya
		Shungura B	3.36–2.85 Mya
		Shungura C	2.85–2.52 Mya
		Shungura D	2.52–2.37 Mya
		Shungura E + F	2.37–2.33 Mya
		Shungura G	2.33–1.88 Mya
		Shungura H	1.88–1.65 Mya
		Shungura K	1.53–1.39 Mya
		Shungura L	1.39–1.12 Mya
Tanzania	Laetoli	Upper Laetoli Beds	3.8–3.5 Mya
	Olduvai	Bed I	1.87–1.7 Mya
		Bed II	1.7–1.2 Mya

\*No Carnivora are known from the Moiti or Lower Burgi Members.

ecological significance of these distributions and made comparisons with the modern fauna. In so doing, they also made interesting use of the method of cenograms (in the original sense of Valverde, 1964) thereby clearly anticipating in a qualitative fashion some current work on the energetics of carnivores (Carbone *et al.*, 1999).

The work of Petter & Howell (1985) was ahead of its time and has not been expanded upon subsequently, perhaps partly because it appeared in a relatively obscure publication and partly because their concern with local palaeoecology has subsequently come to be replaced by an interest in global patterns and determinants of large-scale evolution. Such is the scope of the compilation paper by Turner (1990), the first to provide a figure with stratigraphic ranges for all taxa concerned. This has subsequently become the benchmark paper for the study of African carnivoran evolution, despite the fact that the data for eastern Africa were obtained mostly from the pre-1990 published literature. Turner's paper discusses only larger carnivorans (families Felidae, Hyaenidae and Canidae), for the justifiable reason that they, at least at that time, had a far better fossil record than the smaller carnivorans. Unlike Petter & Howell (1985), Turner (1990) covers the entire Plio-Pleistocene. The evolution of African Carnivora is then set against the backdrop of global change in the Plio-Pleistocene and extinctions and dispersals are discussed in this context. The general conclusion is that the pattern of evolution in the Carnivora in Africa is 'broadly correlated with climatic change and with the evolution of the potential prey species' (Turner, 1990: 349).

A subsequent paper by Turner & Wood (1993), which for carnivores was based on the same data as Turner (1990), provides a refinement in that separate stratigraphic range charts are provided for eastern and southern Africa. The carnivores, along with other mammalian groups, are then discussed in terms of faunal similarity between these two regions, with the conclusion that the Carnivora is the group that shows the greatest similarity between the two regions.

A few years later, Lewis (1997) studied the fossil material of larger carnivorans from some selected stratigraphic units, including Olduvai Gorge, Bed I, and Koobi Fora, Okote Member. Although this study involved first-hand analysis of the specimens, it was limited to just the Felidae, Hyaenidae and Canidae from a subset of eastern African localities. The data were used for ecomorphological analysis and comparison with similar samples from South Africa to better understand ecological shifts in the guild structure through time.

More recently still, Turner *et al.* (1999) have provided a locality-based listing of fossil mammalian taxa of the African Plio-Pleistocene. The larger carnivorans

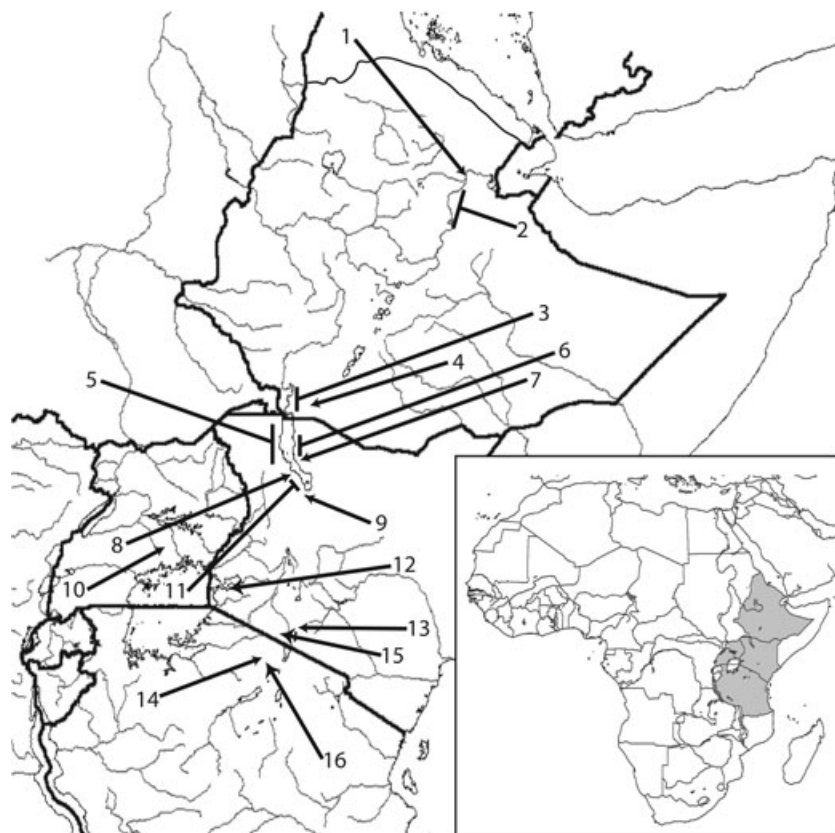
are again taken mainly from Turner (1990), with additions based on literature published after that date. New to this compilation are the smaller carnivorans, the data for which are based on published records. In a separate paper in the same volume, Turner (1999) again discusses biogeographical relationships between the carnivores of eastern and southern Africa, this time focusing on Felidae and Hyaenidae, with the latter being the subject of an in-depth analysis. In Turner (1999), the author's previous conclusion, that the Carnivora is the mammalian group that shows the greatest similarity between eastern and southern Africa, has been further strengthened by new finds of hyenas in eastern Africa.

Most recently, Vrba (2000) has provided a new compilation, this time only at the generic level, of the Neogene mammals of Africa. The carnivoran record in this compilation is based mainly on the same sources as that of Turner *et al.* (1999). Since the scope of her paper is much broader, Vrba (2000) discusses only briefly some immigrations and extinctions. Of interest here is that she pinpoints the fauna of Laetoli as contributing significantly to the first appearance datum points (FADs) in the early to middle Pliocene.

The data presented herein are based on work in progress. This is part of a project that aims at providing a complete revision of the Plio-Pleistocene Carnivora of Africa, with a view to studying the ecomorphological evolution of this group of mammals in a framework of climatic change and competitive structures. Some of this work is published or in press (e.g. Werdelin, 2003a, b; Werdelin & Lewis (2000, 2001), whereas other work as yet exists only in manuscript or as analyses. We find it appropriate to provide this overview at the present time, to illustrate a new view of carnivoran evolution in eastern Africa, which is significantly different from that of the current state-of-the-art as represented by Turner (1990).

This paper is concerned only with eastern Africa. A map showing the localities studied can be found in Figure 1. We hope to provide a similar compilation for southern Africa in the future, but for the time being we shall not be discussing faunal similarities and differences between these two regions.

In the remainder of this paper we shall first provide our compilations in the form of a stratigraphic range chart for all eastern African Plio-Pleistocene Carnivora known to us (Fig. 2). We then discuss these and try to provide some necessary background information regarding specific taxa. This discussion will follow a somewhat similar format to that of Turner (1990). After this, we provide some quantitative data on species richness, origination rates and extinction rates, and a summary of eastern African carnivoran evolution in the Plio-Pleistocene. Our list of extant taxa is based on the distribution maps in Kingdon (1997).



**Figure 1.** Map showing geographical location of localities studied. 1, Hadar; 2, Middle Awash; 3, Omo, Shungura and Usno Formations; 4, Konso-Gardula; 5, West Turkana, Nachukui Formation; 6, Koobi Fora; 7, Allia Bay; 8, Lothagam; 9, Kanapoi; 10, Nkondo/Nyaburu; 11, West Turkana, Eshoa Kakurongori, South Turkwel, Nakoret; 12, Kanam East; 13, Ologesailie; 14, Olduvai; 15, Lainyamok; 16, Laetoli. Inset: map of Africa showing (shaded) countries with localities with carnivoran specimens used in this work.

## THE CARNIVORAN FOSSIL RECORD

This section will be separated into large (families Canidae, Ursidae, Hyaenidae and Felidae) and small (families Mustelidae, Nandiniidae, Viverridae and Herpestidae) carnivoran subheadings. This is not because there is any real division between these two groups (some 'large' carnivorans are a good deal smaller than some 'small' carnivorans), but rather because such a separation has often been used in discussions of African carnivorans (e.g. Turner, 1990). We hope by this means to make it easier for the reader to directly compare our results with previous studies of eastern African Carnivora. All of this discussion can be referred back to Figure 2.

### LARGE CARNIVORANS

#### *Canidae*

The first record of a fossil canid from eastern Africa is an unpublished specimen that probably comes from

the Mursi Fm. of the Omo Group (c. 4–4.5 Mya) (J. Fleagle & F. Brown, pers. comm.). In the Laetoli material, two and possibly three species of canid are known. The *Vulpes* sp. of Petter (1987) is probably identical with the aff. *Canis brevirostris* of Barry (1987), whereas cf. *Megacyon* sp. may be a distinct, much larger, species of *Canis* or a related taxon. We have elsewhere (Werdelin & Lewis, 2000) suggested that the cf. *Canis brevirostris* may belong in the genus *Eucyon*, but R. H. Tedford (pers. comm.) has noted that it may instead be related to *Nyctereutes*, a suggestion also made by Barry (1987). We now agree with this assessment. This lineage is no longer represented in Africa, being restricted to northern parts of Eurasia. A third form at Laetoli may be represented by LAET 4603, referred by Barry (1987) to Canidae genus and species indet. This form shows *Canis*-like features but is considerably smaller than the taxon represented by the cf. *Megacyon* tooth.

The earliest definite *Canis* is from South Turkwel (Werdelin & Lewis, 2000), and specimens of what is



probably the same species have also been found at Hadar, along with material of two smaller *Canis* spp. and a larger canid. Specimens referred to *Canis* aff. *mesomelas* or *C. cf. mesomelas* have been found at several sites in eastern Africa, including Koobi Fora (Leakey, 1976) and West Turkana (Harris, Brown & Leakey, 1988). This material is, except for size, no more similar to *C. mesomelas* than it is to either of the other living jackal species, and thus cannot be referred to any of the living species. In addition, it is worth noting that material referred to *C. mesomelas* from Koobi Fora (Leakey, 1976) and Olduvai (Petter, 1973) is quite distinct dentally, and is likely to represent more than one species. The earliest material referable to the living *C. mesomelas* is from Lainyamok (Potts, Shipman & Ingall, 1988; Potts & Deino, 1995), indicating a late origin for the species. Currently, three species of jackals, *C. mesomelas*, *C. aureus* and *C. adustus*, are present in eastern Africa, but there is no evidence in the fossil record of the region for more than two species of jackal at any given time.

It is notable that the African hunting dog (subgenus *Lycaon*) cannot be positively identified in the fossil record of eastern Africa until the middle Pleistocene of Lainyamok. The earlier record from West Turkana (Harris *et al.*, 1988) is an m1 trigonid which we consider indeterminate. *Canis africanus*, which is considered closely related to *Lycaon*, is known with certainty only from Olduvai, Bed II. The type specimen described by Pohle (1928) is from an indeterminate horizon and the specimen itself is missing. Recently, Martínez Navarro & Rook, 2003) have discussed the *Lycaon* lineage and have synonymized *Canis africanus* with *Xenocyon lycaonoides*, originally described from Gombaszög in Hungary by Kretzoi (1938), with this species as a plausible ancestor for the modern *Lycaon pictus*. The earliest record of the latter is from Hayonim Cave in Israel (Stiner *et al.*, 2001). This scheme seems plausible, although it must be noted that leaving *Lycaon* with full generic status renders *Canis* paraphyletic. In view of this and pending a revision of the genus *Canis*, we prefer to refer these species, as well as the ancestral species of the lineage '*Lycaon*' *falconeri*, to *Canis*. In addition, material from South Africa suggests a relatively recent origin for the modern species (Lewis & Berger, 1998).

*Otocyon* is another canid genus with a FAD at Lainyamok. Its putative ancestor, *Prototocyon recki*, is known from Olduvai, Bed I. A possible record of *Fenecus* is known from Koobi Fora (Upper Burgi or KBS Mb.), but the specimen in question is a small fragment and the record doubtful enough that we have left it out of the present listing.

Overall, canids are scarce in the fossil record of eastern Africa, a fact probably explained by their overall preference for open habitats. Most of the fossil sites

sampled for carnivorans in the region lay near substantial bodies of water, implying that the immediate surroundings may have had relatively closed vegetation.

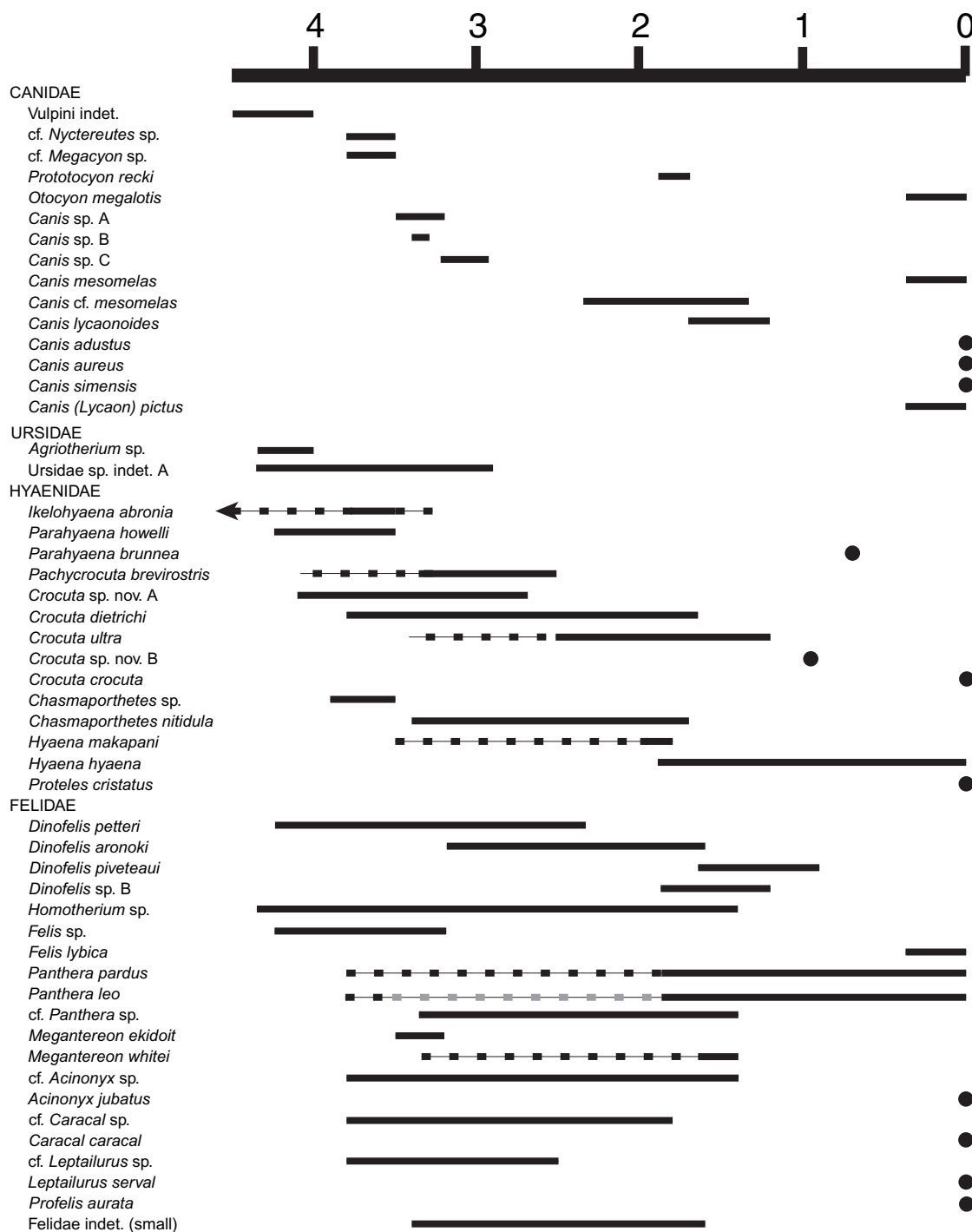
#### *Ursidae*

The first report of Ursidae in the Plio-Pleistocene of eastern Africa was the identification of *Agriotherium* sp. from Aramis (WoldeGabriel *et al.*, 1994). The presence of *Agriotherium* in the Pliocene of the region is not entirely surprising, given its presence in Langebaanweg, South Africa, at the beginning of the epoch, as well as its presence in late Miocene deposits of Ethiopia (Haile-Selassie, 2001). More surprising is the presence of at least one species of ursine bear. The definite record of this bear reaches to c. 2.9 Mya. Material of this species from the Denen Dora and Kada Hadar Mbs at Hadar, the Tulu Bor Mb. at Koobi Fora and the lower Lomekwi Mb. of West Turkana is very large, though not as large as *Agriotherium africanum* from Langebaanweg. With at least two species now known, we may conclude that bears were, if not common, at least a notable presence in the early Pliocene of eastern Africa. Today, bears are known only from the northernmost parts of Africa.

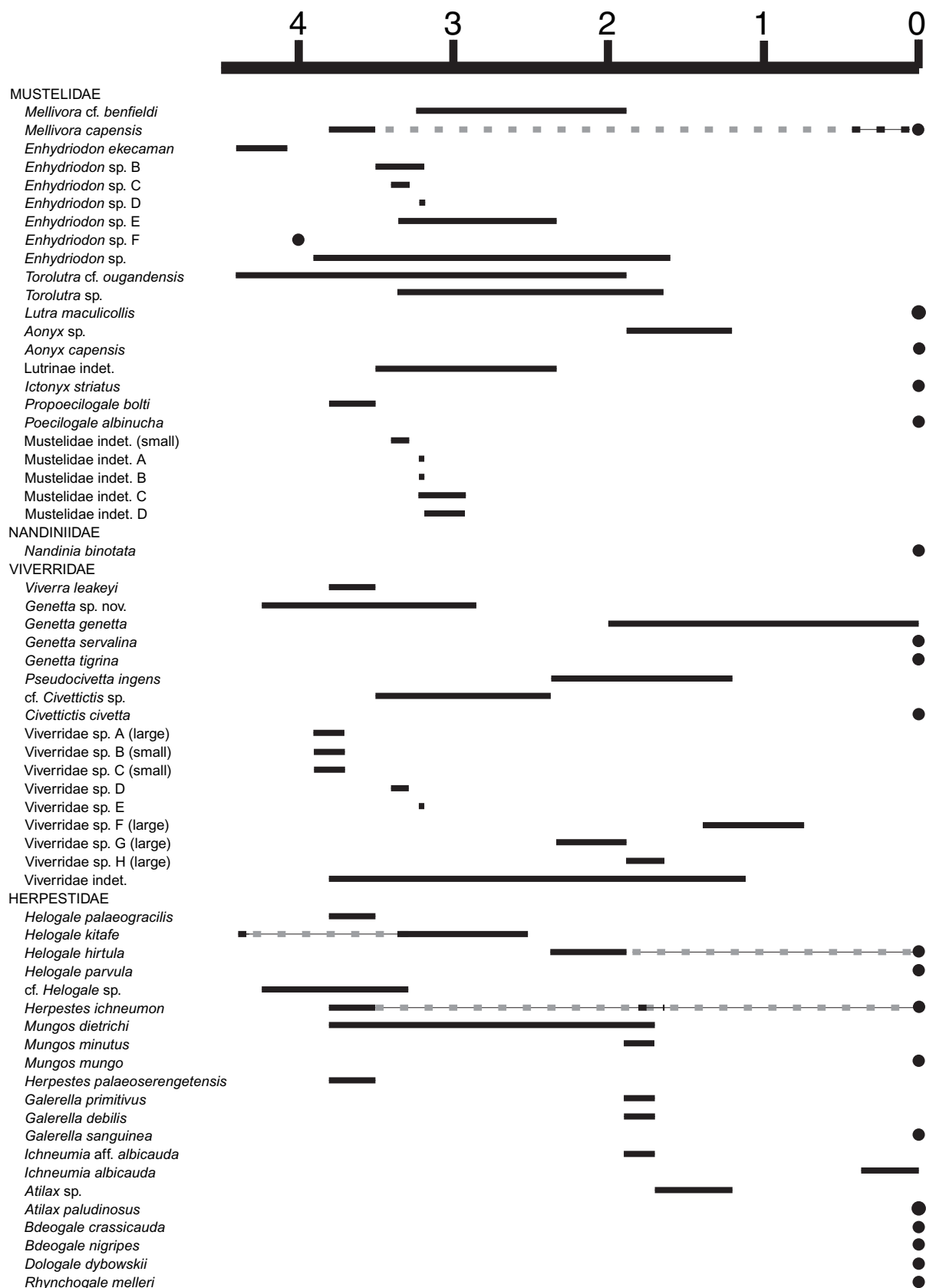
#### *Hyaenidae*

The absence of specialized, bone-cracking hyenas in the Miocene and earliest Pliocene of Africa has been commented upon elsewhere (Werdelin & Turner, 1996a; Turner, 1999). The earliest species in this category (morphotype 6 of Werdelin & Solounias, 1996) is *Parahyaena howelli* from Kanapoi, an early relative of the living brown hyena. The earlier suggestion by Howell & Petter (1980) that the Kanapoi hyena belonged in *Pachycrocuta* was correctly discounted by Turner (1990). This species is also known from several other sites, including Laetoli (specimens LAET 3951 and 1618 and others; cf. Barry, 1987). Referral to *Parahyaena* becomes more plausible with the identification of the living brown hyena in the middle Pleistocene of Kenya (Werdelin & Barthelme, 1997). The brown hyena is presently known only from southern and south-western Africa.

The living striped hyena, *Hyaena hyaena*, appears at about 1.9 Mya, but is immediately preceded by the ancestral form, *H. makapani*. This species (or a species closely similar to it) first appeared as far back as c. 3.5 Mya, in the Lokochot Mb. at Koobi Fora. *Hyaena makapani* is smaller and more gracile than the living species, showing fewer adaptations to bone-cracking. *Hyaena makapani*, in turn, differs from *Ikelohyaena abronia* essentially only in the loss of m2 and M2, suggesting that the independent generic status of the lat-



**Figure 2.** Stratigraphic ranges of eastern African Carnivora on which the analyses in this paper are based. The horizontal scale is in millions of years. Solid lines indicate a confirmed fossil record. Dashed black lines indicate an uncertain record. Dashed grey lines indicate an inferred record because of presence before and after this time (range-through taxon). An internal dot indicates a taxon known only from a site with a very brief temporal extent. A terminal dot indicates a taxon with no known fossil record in eastern Africa.



ter should be re-evaluated. *Ikelohyaena abronia* may be a Miocene holdover, with its earliest possible occurrence at Lothagam and its latest either at Laetoli (positive identification, specimens LAET 3338 and 1849) or in the Sidi Hakoma Mb. at Hadar (tentative identification of a very worn specimen). The striped hyena is widespread in eastern Africa today.

The history of the spotted hyenas, genus *Crocota*, is complex, both in eastern Africa and elsewhere. Authors such as Ewer (1954a, b) and Petter (1973) have used the species name *C. ultra* for late Plio-Pleistocene spotted hyenas in both eastern and southern Africa. More recently, Barry (1987) suggested that the spotted hyena of Laetoli might be a distinct species, possibly related to the Asian *C. sivalensis*. This suggestion was formalized by Petter & Howell (1989) when they coined the name *C. dietrichi* for the Laetoli *Crocota*. These suggestions for splitting up *Crocota* have been argued against by several authors (Turner, 1990; Werdelin & Turner, 1996a), who thought that both *C. ultra* and *C. dietrichi* could fit comfortably within the range of variation of the living species. We now believe that both of these species are valid, although for partly different reasons than those cited by previous authors on the subject (M. E. Lewis & L. Werdelin, unpubl. data). In addition, we have evidence for the presence of at least one and possibly two other species of *Crocota* in the Plio-Pleistocene of eastern Africa. A specimen from the lowermost part of the Lomekwi Mb. of the Nachukui Formation in West Turkana (KNM-WT 40481) is nearly as old (c. 3.3 Myr old) as the oldest *C. dietrichi* and has a very different morphology, indicating that the earliest evolution of *Crocota* must be reconsidered. This species is likely also present at Hadar (Denen Dora Mb.) and in the Tulu Bor Mb. at Koobi Fora (KNM-ER 3748, previously referred to *Pachycrocota*; Werdelin, 1999). *Crocota dietrichi* is now identified as late as the KBS Mb. at Koobi Fora (KNM-ER 1539). *Crocota ultra* is definitely present in the Lokalalei Mb. in West Turkana (KNM-WT 39209), but may also have been present in the earlier Lomekwi Mb. Its last appearance is in Olduvai, Bed II. A possible second new species is known from Ologesailie, although this may be a geographical or temporal variant of *C. ultra*. Whether the *Crocota* from the Daka Mb. of the Bouri Fm. of the Middle Awash Valley reported by Gilbert (2003) belongs to this species (they are of approximately the same age) remains to be seen. The living species, though currently common and widespread, is not known in the fossil record of eastern Africa.

The earliest record of *Chasmaporthetes* in eastern Africa is from Allia Bay (c. 3.9–3.7 Mya). The genus is also reported from Laetoli (Turner, 1990), although we are unconvinced of the specific attribution to *C. silberbergi*. The species *C. nitidula* is known on the

basis of good, diagnostic material from Hadar and Olduvai.

The presence of *Pachycrocota* in eastern Africa has been discussed elsewhere (Werdelin, 1999). The specimen from the Tulu Bor Mb. at Koobi Fora referred to in that paper must be removed from the sample, however. We now believe that it may belong to the new species of *Crocota* discussed above.

Overall, there were more scavenging and bone-cracking hyenas around in the past than today. However, this does not automatically mean increased support for the hypothesis of community coevolution between hyenas and sabretooth felids (Ewer, 1967; see Discussion in Turner, 1999), because the extinctions of the hyenas are decoupled from those of the sabretooths (see below).

### Felidae

A substantial literature on the Plio-Pleistocene felids, and especially the sabretooths (subfamily Machairodontinae), has accumulated over the years. Much of this literature has concerned their role as providers of carcasses for the suggested scavenging behaviour of early hominins, and has necessarily concerned the extinction of sabretooths in Africa in the early to middle Pleistocene. Less attention has been paid to changes within lineages of cats, which, though subtle, certainly had an impact on the types and quantities of carcasses these cats may have provided for the scavenging guild (including early hominins).

The eastern African Plio-Pleistocene sabretooths belong to three different tribes, the Metailurini (the genera *Dinofelis* and possibly *Metailurus* are present in eastern Africa), the Smilodontini (the genus *Megantereon* is present in eastern Africa), and the Homotheriini (the genus *Homotherium* is present in eastern Africa). Members of the three tribes are functionally and ecologically distinct. The genus *Dinofelis* has recently been revised by us (Werdelin & Lewis, 2001) and we now recognize five species in eastern Africa, including one from Lothagam which is not included in the present analysis. Of the remaining four, one is known only from Olduvai (*Dinofelis* sp. B). The most common of the remaining species is *D. petteri*, which is known from a number of localities from Kanapoi to Omo, Shungura Fm., Mbs E + F. A rarer species is the transitional *D. aronoki*. This species is known from a few localities, ranging from the Kada Hadar Mb. at Hadar and the Kaiyumung Mb. at Lothagam, to the unpublished site of Nakoret, west of Lake Turkana. The last species is *D. piveteaui*, originally described from southern Africa, which is known from the Okote Mb. at Koobi Fora, Konso-Gardula and Kanam East. The latter record has been discussed by Ditchfield *et al.* (1999) and tentatively placed as recently as



c. 0.9 Mya, which, if correct, would make this the youngest record of a sabretooth in Africa.

The record of *Metailurus* in eastern Africa is extremely tentative. There is one possible identification from the Miocene levels at Lothagam (Werdelin, 2003b) and one even more tentative identification from Olduvai, Bed II (Petter, 1973). A third possible record is from Hadar. These finds are all fragmentary or damaged, making firm identification very difficult. However, they all appear to record the presence in eastern Africa of a sabretooth felid smaller than any known *Dinofelis*. The link to *Metailurus* is based in part simply on size, and in part on the presence of an undoubted Metailurini at Langebaanweg in South Africa. This record was described as '*Felis*' *obscura* by Hendey (1974). Turner *et al.* (1999) list *Adelphailurus* sp. from Langebaanweg, which must be a reference to this taxon, cf. Turner & Antón (1997). *Adelphailurus* is a North American metailurine. The main difference between this genus and *Metailurus* lies in the presence of serrations at the base of the anterior and posterior crests of the upper canine in *Adelphailurus* (Hibbard, 1934; Harrison, 1983). Such serrations are absent in *Metailurus* and in '*F.*' *obscura* as well, indicating that referral to *Adelphailurus* is incorrect. Whether '*F.*' *obscura* should be referred to the genus *Metailurus* or not is impossible to answer without renewed, detailed study. We have not shown the tentative record of *Metailurus* in eastern Africa in the stratigraphic range charts, as further material is required to confirm the presence of the genus.

The earliest possible record of *Megantereon* in Africa is from Aramis (WoldeGabriel *et al.*, 1994), but a description or discussion of this material has yet to be published. The earliest certain record is from South Turkwel, from which we have recently described a new species, *M. ekidoit* (cf. Palmqvist, 2002, and Werdelin & Lewis, 2002, for a discussion of this taxon). *Megantereon* is known from many sites in eastern Africa. Unfortunately, most finds are of isolated teeth, which are insufficient to distinguish between *M. ekidoit* and the successor species, *M. whitei* (cf. Martínez Navarro & Palmqvist, 1995, 1996 for a discussion of the nomenclatorial status of African *Megantereon*). The only definite record of *M. whitei* in eastern Africa is from the Okote Mb. at Koobi Fora and we cannot at present say when the transition between these two forms occurred.

*Homotherium* sp. is known from many sites from the early Pliocene onwards. The earliest records are from Kanapoi and the Lonyumun Mb. at Koobi Fora, but the species is not listed as present at Aramis (WoldeGabriel *et al.*, 1994), which may or may not be significant from an ecological or evolutionary perspective. A related genus, *Lokotunjailurus*, has been found at Lothagam (Werdelin, 2003b). Recent finds of

*Homotherium* from the Okote Mb. at Koobi Fora (dated 1.64–1.39 Mya), represent its last certain record in eastern Africa.

Thus, the extinction of the sabretooths in eastern Africa cannot be demonstrated to have been linked to a common cause (*pace* Turner, 1990, 1999, and Turner & Antón, 1997; but see also Lewis, 1996). *Megantereon* and *Homotherium* may have become extinct more or less simultaneously. However, if the dating of the *Dinofelis* at Kanam East is correct, this genus must have become extinct later than the other two.

Both the lion and the leopard have putative first appearances at Laetoli (Barry, 1987; Turner, 1990). However, neither of these records is particularly well substantiated, although the 'leopard' is somewhat better represented than the 'lion'. The lion record of Laetoli consists of a broken maxilla fragment with P3 and broken P4, an edentulous mandible fragment, a few fragments of carnassials, some incisors, and a few postcranial bones. Essentially, all that can be said of these is that they pertain to a *Panthera*-like felid the size of a small lion. Barry (1987) suggested a number of possibilities and settled for calling this material '*Leo* (= *Panthera*) aff. *gombaszoegensis* or *L. palaeosinensis*'. He was very clear in stating that the Laetoli form was specifically different from either of these, as well as from the lion. Turner (1990), on the other hand, suggested that 'neither [Barry's] discussion nor his illustration . . . give reason to identify the material as anything other than lion.' This is quite true, as far as it goes, because the material is, indeed, more similar to lion than to any other suggested taxon. However, the point here is that the material is hardly diagnostic at the species level. In addition, we must take into account the possibility of an ancestral species being present 3.5 Mya in eastern Africa. This possibility is given additional weight by the subsequent fossil record of lions in the region. Their first definite appearance is at Olduvai, Bed I, which is nearly 2 million years later than the Laetoli record. Turner (1990) reports Howell & Petter (1976) as recording lions from the Shungura Fm., Mb. G, but the only reference to lions in the latter paper is from Mb. L. All of the material from Mb. G that we have studied is too small to be lion, while that from Mb. L is very similar to the living *P. leo*. Most of the material referred to 'Felinae indet. (lg)' from the Usno Fm. and Shungura Mbs C, D and F by Howell & Petter (1976) pertains to *Dinofelis*, with a few pieces belonging to *P. pardus*. At Koobi Fora, the earliest lion material is from the Okote Mb. Thus, there is a large hiatus in the lion record, suggesting that the taxonomic status of the Laetoli material should be reviewed. We have here nonetheless left it as *P. cf. leo*.

The leopard material from Laetoli is more extensive and the referral to *P. cf. pardus* more justified. The

record of leopard or leopard-like specimens in eastern Africa is more continuous than that of lions, especially in the Shungura Fm. of the Omo Group. However, the first definite record is from Olduvai, Bed I, while older specimens are relatively fragmentary and more difficult to assign with certainty to this taxon.

The genus *Acinonyx* is yet another taxon with its first appearance at Laetoli. Subsequently, material of the genus is found infrequently but consistently in the Omo sequence until about 2.5 Mya. These specimens are larger than the living species and appear unlikely to be conspecific with it. The last occurrence of cheetah in eastern Africa before the present is from the Okote Mb. at Koobi Fora.

Smaller cats are, not surprisingly, rare in the fossil record of eastern Africa. Material identical, or closely related, to the modern caracal is found at Laetoli, Omo Shungura Fm., Mb. B, the Upper Burgi Mb, Koobi Fora, and Pinnacle at Hadar. Material similarly tentatively associated with the living serval is found at Laetoli and the Kaiyumung Mb., Lothagam. Material likely to belong in the genus *Felis sensu stricto* is found at Kanapoi, the Denen Dora Mb., Hadar, and Lainyamok. Finally, small indeterminate cat material has been found at several sites between c. 3.4–1.6 Mya. This material is not included in the analyses.

In summary, the fossil record of cats in eastern Africa shows sabretooths to be more or less ubiquitous, with *Dinofelis* the most common, followed by *Homotherium* and with *Megantereon* as the rarest. Even the latter is more common than either lion or leopard, however. These patterns obviously reflect differences in habitat preference, but it is less obvious how they should be interpreted. Like the situation with canids, the felid pattern may represent adaptive differences along the open habitat/closed habitat continuum. There is apparently no concerted extinction of sabretooths around 1.5 Mya, despite previous assertions to the contrary. Most surprising, perhaps, is the scarcity of lion-sized material of *Panthera* throughout the sequence.

#### SMALL CARNIVORANS

##### *Mustelidae*

The most important feature of the mustelid Plio-Pleistocene fossil record of eastern Africa must surely be the extensive radiation of Enhydrini ('sea otters'). This radiation commenced in the latest middle and upper Miocene with the genus *Vishnuonyx*, known from the Ngorora Fm. (Hill *et al.*, 1985) and from lower levels at Lothagam (Werdelin, 2003b). The successor genus, *Enhydriodon*, first appears in the Lukeino Fm. (upper Miocene). This genus then radiates extensively in eastern Africa in the Pliocene, with a representative also appearing in southern Africa (Stromer, 1931;

Hendey, 1974, 1978). Looking at the six species on the stratigraphic range chart, most of which have brief stratigraphic ranges, it may appear that the genus has been oversplit. However, given the plausible scenario that this radiation occurred in isolated drainage basins of lakes and small or large rivers, each with its specific fish fauna, it is not unreasonable that a group of aquatic carnivorans should evolve into a series of local species, each with a particular set of adaptations to its environment and prey, and that these species should be of relatively short duration, as they would be dependent on the history of the hydraulic systems in which they lived.

In terms of morphology, the different species of *Enhydriodon* are as different as any congeneric species of carnivorans could be. There is a great temporal increase in size from the earliest, otter-sized forms, to massive giants with limbs the size of a lion's towards the end of the genus' history. Coeval species tend to have quite distinct dental adaptations. As noted, *Enhydriodon* is first known from the Lukeino Fm. (c. 6–5 Mya). The first Pliocene record is from Sagatya A, a locality probably coeval with Kapthurin, i.e. c. 4.4 Mya (A. Hill, pers. comm.). The same species (*Enhydriodon ekecaman* Werdelin, 2003; listed as *E. pattersoni nomen nudum* in Turner *et al.*, 1999) is also known from Kanapoi. The last occurrence of material referable to a specific species is from the Shungura Fm., Mbs E + F, while the last occurrence of material referable to the genus *Enhydriodon* is from Nakoret, i.e. from before 1.6 Mya. There is as yet no plausible scenario to account for the enormous increase in body mass during the evolution of the lineage, but the extinction of *Enhydriodon* must surely be linked to the changes in the drainage patterns of the palaeolakes and palaeorivers in eastern Africa that occurred with the gradual aridification of the latest Pliocene and early Pleistocene.

Several other lutrine species are known. There are two members of the Lutrini which, for convenience here, are both referred to the genus *Torolutra*. One of these is of a size and morphology comparable to *T. ougandensis*. This form, which we refer to *T. cf. ougandensis*, is known from Aramis and has its last occurrence in the Upper Burgi Mb. at Koobi Fora. The other form is smaller and more *Lutra*-like and occurs in deposits from the Lomekwi Mb. in West Turkana to the KBS Mb. at Koobi Fora. *Aonyx* sp. is known from the Kakesio Beds at Laetoli, while Petter (1973) has tentatively identified *Aonyx* sp. from Olduvai, Beds I and II. We accept this identification and here assume that this is the same material that Turner *et al.* (1999) refer to *Lutra maculicollis*. Other material of *Aonyx* sp. is known from the KBS Mb. at Koobi Fora. In addition to these records, material of indeterminate Lutrinae is known from South Turkwel (Werdelin & Lewis,

2000), several Shungura Fm. Mbs, and the Lomekwi Mb. of West Turkana.

The melliivorines have an interesting distribution in the fossil record. At Lothagam there is material referable to a more primitive species than the living form (Werdelin, 2003b). At Laetoli, Petter (1987) described a specimen of *Mellivora* of the size of the living species, *M. capensis*. However, at Hadar and Koobi Fora there is material of *Mellivora* that is distinctly smaller than the living species, more akin to *M. benfieldi* from Langebaanweg (Hendey, 1978). Several possibilities exist: (i) the material from Laetoli represents a different species from either *M. benfieldi* or *M. capensis*, possibly identical to that from Lothagam; (ii) two species of *Mellivora* were present simultaneously throughout the upper Pliocene and lower Pleistocene; or (iii) all the material from Laetoli onwards represents one highly plastic lineage. The latter is the solution suggested by Petter (1987). This issue requires additional work for its resolution. In the quantitative compilations below we have counted only one species of *Mellivora* in existence at any one time. The living *M. capensis* has a wide distribution in Africa and Asia.

Material belonging to the smallest Mustelidae is limited, except at Hadar. Petter (1987) identified *Propoecilogale boliti*, an ancestral striped weasel, from Laetoli. Hadar harbours several small species of mustelids in several members, but work on identifying these is not yet completed. Nevertheless, the presence at Hadar of these species is likely to be of significance to palaeoecological reconstructions.

Overall, the mustelid fossil record in eastern Africa suggests a trend from many aquatic forms to fewer ones, which is in keeping with reconstructions of the changes in the palaeoclimate of the region in the Plio-Pleistocene.

#### *Nandiniidae*

The palm civet, *Nandinia binotata*, is here placed in its own family in view of the diverging opinions regarding its phylogenetic position (Flynn & Nedbal, 1998; Gaubert, Veron & Tranier, 2002; Hunt, 1974). Neither the species nor the genus has a fossil record in eastern Africa.

#### *Viverridae*

The Viverridae is a complex group with a limited fossil record. The most interesting aspect of its record in eastern Africa is the presence of several quite distinct species of large-bodied viverrids in the Plio-Pleistocene. By large-bodied we here mean taxa that were at least twice the body mass of the living African civet, *Civettictis* (or *Viverra*) *civetta*. One such species is *Pseudocivetta ingens*, described by Petter (1967, 1973)

from Olduvai, Bed I. This specialized and very distinctive species is now also known from the Upper Burgi and KBS Mbs at Koobi Fora and in the Shungura Fm., Mbs E + F and G, as well as from Olduvai, Bed II. It is thus by no means an uncommon form. An older large-bodied form is *Viverra leakeyi* from Laetoli (Petter, 1963, 1987). This species, or one similar to it, is also present at Lothagam. Other large viverrid taxa are known from Allia Bay and the KBS and Chari Mbs at Koobi Fora. Though substantial in size, the Allia Bay form is too small to fit comfortably with the *V. leakeyi* specimens. The KBS Mb. specimen is represented by a complete skull with dentition (KNM-ER 5339) that is quite different from that of any known viverrid, but is probably closest to *Civettictis*. The Chari Mb. viverrid is represented by an occipital region of the skull that is completely different in its construction from the KBS form, although at present it cannot be excluded that this is a late surviving *Pseudocivetta*. Material more akin to the extant *Civetta* in size and morphology is known from several areas, including West Turkana, Hadar and Omo. Owing to taxonomic uncertainties, this material has not been included in the analyses.

Two species possibly related to *Genetta* are known from Lothagam (Werdelin, 2003b) and at least one species from the late Miocene deposits of the Middle Awash can probably be referred to this genus (Haile-Selassie, 2001). The first definite record of the genus *Genetta* is from Kanapoi, however. What is likely to be the same species is also known from the Shungura Fm., Mb. B. The extant *G. genetta* is, on the other hand, first known from the Okote Mb. at Koobi Fora.

Unidentified small viverrids are known from a few sites. Interestingly, Allia Bay has two or three species of small viverrids, none of which can be assigned to the same taxon as the *Genetta* sp. from Kanapoi. There are three distinct morphs at Allia Bay, but two of these might be the two sexes of the same species. Only more study will resolve this issue. There are also small viverrids present in the Sidi Hakoma and Denen Dora Mbs at Hadar. Finally, Viverridae material not definitely assigned to a species or morphotype is known from many sites, from Laetoli to the Shungura Fm., Mb. L but has not been included in the analyses.

Overall, the record of viverrids can at best be described as patchy. There seems to be a greater abundance of smaller, probably arboreal, forms early in the record and more of the large, probably terrestrial, forms later. This would match the palaeoclimatic record of a gradual aridification, reduction in tree cover and spread of the savanna biome.

#### *Herpestidae*

The fossil record of Herpestidae in the Plio-Pleistocene of eastern Africa is similarly patchy. There have been



no extinct genera described in this time period and the first definitely recognized of the modern genera is *Helogale*, with *H. aff. kitafe* reported from the Adu Asa Fm. of the Middle Awash (Haile-Selassie, 2001) and *H. cf. kitafe* from Aramis (WoldeGabriel *et al.*, 1994). An indeterminate member of this genus is also known at Kanapoi. The first fossil species of a Pliocene herpestid from Africa to be described was *H. palaeogracilis* from Laetoli (Dietrich, 1942). A second fossil species, *H. kitafe*, was subsequently described from the Omo by Wesselman (1984), who also reported the presence of the extant Somali dwarf mongoose, *H. hirtula*, from younger Members of the Omo sequence. The other extant species, the dwarf mongoose, *H. parvula*, is not known as a fossil.

A species tentatively assigned to *Herpestes* sp. has been recorded from the Adu Asa Fm., Middle Awash (Haile-Selassie, 2001), although this generic attribution seems questionable. The Egyptian mongoose, *H. ichneumon*, has a sparse record, starting with Laetoli (Petter, 1987), and with a possible later occurrence at Olduvai (Petter, 1973). It has not been observed in the Omo or in the formations to the east and west of Lake Turkana.

An extinct relative of the banded mongoose, *Mungos dietrichi*, is known from Laetoli, West Turkana and Olduvai, while a second, smaller species has been reported from Olduvai (Petter, 1973). The extant banded mongoose, *M. mungo*, is not known as a fossil.

We are here using *Galerella* at the generic rather than subgeneric level. This genus has been recorded from three extinct species, *G. palaeoserengensis* from Laetoli and *G. primitivus* and *G. debilis* from Olduvai. However, recent work (R. Dehghani & L. Werdelin, unpubl. data) suggests that the former should be referred to *Herpestes sensu stricto*. The extant slender mongoose, *G. pulverulenta*, has not been observed in the fossil record.

The white-tailed mongoose, *Ichneumia albicauda*, has doubtful records from Bed I at Olduvai and from Lainyamok. The fossil record of the marsh mongoose, *Atilax paludinosus*, is restricted to Olduvai, Bed II. The remaining mongoose genera, *Bdeogale*, *Rhynchogale* and *Dologale* are rare, sparsely distributed, or highly habitat specific today and neither is known from the fossil record.

Overall, the mongoose fossil record in eastern Africa is very strongly dominated by the Laetoli and Olduvai material, making it difficult to interpret. It may be significant that mongooses are absent from Hadar, where the smaller carnivorans are mustelids or viverrids, while the opposite is true of Laetoli and Olduvai. This difference would seem to be in keeping with prevailing views of the development of the eastern African palaeoclimate, which would leave more available space for the terrestrial mongooses later in the record

in association with the development of the savanna biome.

## QUANTITATIVE ANALYSIS

The known record of Plio-Pleistocene Carnivora of eastern Africa as outlined above (Fig. 2), can now be analysed quantitatively. Because we are dealing exclusively with eastern Africa, all data should be interpreted as providing local richness, origination and extinction rates only. We will not be discussing dispersal patterns here, as this would require similar reviews of the southern and northern African records, a task which has yet to be completed. We hope to return to these topics in subsequent work that incorporates other parts of Africa, as well as Eurasia. We have also not focused on palaeoecology, beyond the few words already said above, as this would require more in-depth consideration of different localities and times than is feasible here. Thus, the following analyses will focus exclusively on diversity and turnover patterns. Much has been made of this topic in recent years (e.g. Behrensmeyer *et al.*, 1997; Turner, 1990, 1999; Vrba, 1985, 1988, 1995). These discussions have tended to centre on the turnover-pulse hypothesis of Vrba (1985) because its clear formulation can generate testable predictions. There has been no very clear statement regarding the carnivoran fossil record in this respect, but Turner (1990: 349) has suggested 'broad correlations with the patterns of climatic change and the evolution of potential prey species.' Taking this in conjunction with the suggestion of Turner (1999: 79) that 'it would be reasonable to expect a series of events following a major climatic event, as the vegetation responded and in turn provoked a reaction among the ungulates dependent on it and thus, eventually, among the larger carnivores', we might hypothesize that a turnover event in carnivorans may be present, but would postdate a similar event in the prey species.

## MATERIAL AND METHODS

The material used in this analysis consists of the many hundreds of specimens of Carnivora found at Plio-Pleistocene sites in eastern Africa. Nearly all of these have been studied and identified by us. The exceptions (e.g. Aramis, Konso-Gardula) are of little importance to the following discussion, because they either lie in a time interval that is not analysed further due to sampling issues (e.g. Aramis) or include carnivorans that are known elsewhere from the same time-slices (e.g. Konso-Gardula). Thus, the identifications are based on a uniform view of morphology, taxonomy and systematics, one in which craniodental and postcranial data have been treated equally. This is unlike previous studies of the eastern African record,

which have been based on identifications made by many different scientists, with different views of their material. We do not claim that our identifications necessarily represent 'the truth', but for the purposes of this review, they provide a uniform baseline for the entire study material.

Each taxon has been assigned a FAD and a LAD based on the oldest and youngest ages of the oldest and youngest localities from which it has been identified (Fig. 2). In eastern Africa, these localities are usually the members of the different geological formations in the region, and these members normally have well constrained dates associated with them (e.g. Feibel, Brown & McDougall, 1989; Walter & Aronson, 1993). After FADs and LADs were assigned, the data were binned into intervals of equal length. Herein we have used bin lengths of 300, 400 and 500 kyr. Preliminary analyses showed that the material was not sufficient for a bin length shorter than 300 kyr, while 500-kyr bins were used as this has been a common bin length in similar studies in the past. Data on 400-kyr bins is provided as a check that the results are uniform across bin lengths. As will be seen, the results for all bin lengths are broadly similar. The shorter, 300-kyr bins will be emphasized, however, because these provide more detailed information than the 400- and 500-kyr bins.

All named eastern African carnivoran species are included in the study. Unnamed species have been incorporated where verified by the present authors as being different from all other known species in the material. Thus, *Dinofelis* sp. B from Olduvai is counted as a separate taxon, because, despite not being formally named, it is clearly distinct from all named species of *Dinofelis* (Werdelin & Lewis, 2001). In other cases, however (e.g. the undescribed *Enhydriodon* sp. from Eshoa Kakurongori), the material in question may be conspecific with other material of the same age, and these are therefore counted as one taxon. In this way, we have attempted to provide a minimum estimate of the number of species in the data set. But it also means that the numbers do not match a direct quantification of Figure 2.

We have chosen to analyse the binned data using the methodology developed by Foote (2000). This requires a separation of the taxa in each bin into four categories: those that exist only in that interval ( $N_{FL}$  in Foote's terminology), those that originate before the interval but go extinct within it ( $N_{BL}$ ), those that originate in the interval and persist beyond it ( $N_{FI}$ ), and those that originate before the interval and persist beyond it ( $N_{BI}$ ). For the purposes of this paper, taxa that are present in a bin but not in the preceding one are assumed to have originated within their first observed bin, while taxa that exist in a bin but not in the following one are assumed to have become extinct within their last observed bin. Foote (2000) discusses

the properties of his metrics in some detail and we refer the reader to his work. Specific problems with the metrics due to deficiencies of our data are discussed on a case-by-case basis below.

We are aware of the weaknesses of the African Plio-Pleistocene record and of the problems involved in using it to assess the tempo and mode of mammalian evolution (White, 1995; McKee, 2001). Indeed, it is possible that the carnivoran fossil record of Africa may never meet the standards required of the approach taken by McKee (2001) to be useful in testing hypotheses of tempo and mode, despite the fact that the number of taxa presented herein is about the same as that used by Behrensmeyer *et al.* (1997) in their analysis of late Pliocene turnover in the Turkana Basin. A particular problem with the carnivoran data set is that the number of specimens per taxon is much less than for other mammals, such as bovids and suids. The carnivoran record would thus never allow for studies based on abundance, such as those of Barry *et al.* (2002), Bobe, Behrensmeyer & Chapman (2002) and Bobe & Eck (2001). Nevertheless, suggestions have been made (Turner, 1990, 1999) that the carnivoran Plio-Pleistocene record of Africa provides some – albeit limited – support for the existence of a turnover pulse around 2.5 Mya. Our aim here is thus not to distinguish between possible causes of the observed pattern of carnivoran diversity and diversity change in the African Plio-Pleistocene, but rather to present that pattern simply on the basis of the most up to date and consistent evidence, and to assess whether it may provide support for the hypothesized relationship between environmental and faunal change around 2.5 Mya.

#### THE QUALITY OF THE RECORD

The issue of the quality of the fossil data relative to the research questions at hand is a contentious one with no firm answer. As noted above, applying the quality criteria of McKee (2001) may result in the mammalian fossil record of eastern Africa (let alone the carnivoran one) never being adequate for the task envisaged. However, any model such as that of McKee is at the mercy of its boundary conditions, which increases the level of uncertainty in the system beyond that of the data itself. We prefer to search for signs of sampling adequacy (or inadequacy) in the data themselves, even though such a search may often become circular (the inadequacy of the record may itself make the record appear adequate in some circumstances).

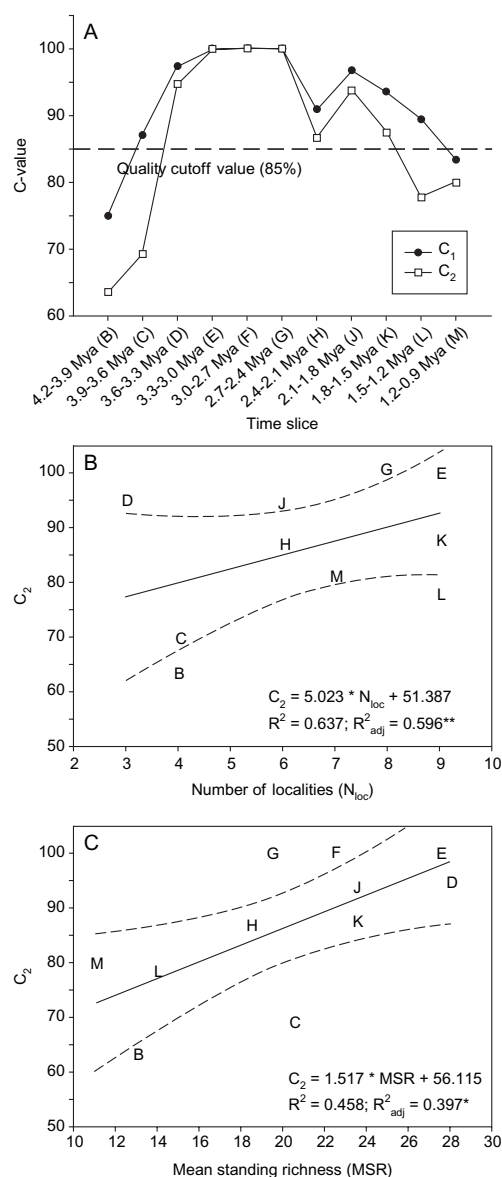
We will here consider sampling adequacy in two steps. In this section, we will consider adequacy as discussed in Maas *et al.* (1995), while in the results section we will consider the question of sampling bias by



looking at the relationship between diversity and number of localities. Maas *et al.* (1995) suggest two completeness indices for sampling adequacy, both based on the proportion of range-through taxa (taxa present before and after an interval, but absent from it; such taxa are generally viewed as having occurred in the interval but not having been sampled). Their first index (their CI, here given as  $C_1$ ) is calculated as  $C_1 = (N_{\text{tot}} / (N_{\text{tot}} + N_{\text{rt}})) * 100$ , where  $N_{\text{tot}}$  is the number of taxa actually found in an interval and  $N_{\text{rt}}$  is the number of range-through taxa reconstructed as having occurred in the interval. The second index (their  $C_{\text{bda}}$ , here given as  $C_2$ ) is calculated as  $C_2 = (N_{\text{bda}} / (N_{\text{bda}} + N_{\text{rt}})) * 100$ , where  $N_{\text{bda}}$  is the number of taxa found before, during and after an interval (i.e. excluding taxa with first and/or last appearances in the interval). In their work, Maas *et al.* (1995) suggest an index of 70 to be a useful *ad hoc* cutoff point for their data, with a higher value indicating reasonably adequate sampling.

It might be expected that carnivorans, which typically are rare in the fossil record and tend to have few fossil specimens per taxon identified, would have a relatively large number of range-through taxa and hence low values of the completeness indices. However, Figure 3A shows that this view is mistaken. Using the more generous  $C_1$  index, no time slice in the data (using 300-kyr bins) has a value below 0.7 and if the more conservative  $C_2$  index is used, only two time slices at the beginning of the interval studied (where it is known that sampling is poorest) have values below 0.7. For the purposes of this paper, a value of 0.85 for the  $C_2$  index can be used as a marker value; time slices with  $C_2$  values below 0.85 should be treated circumspectly in the results and discussions below. That these indices provide something at least akin to a measure of sampling adequacy is indicated by Figure 3B, in which the  $C_2$  value for each time slice is plotted against the number of 'localities' studied in that time slice (here and elsewhere in this paper a 'locality' in reality represents a member or equivalent of a geological formation, such as the Tulu Bor Mb. of the Koobi Fora Fm. or the Denen Dora Mb. of the Hadar Fm.; in this usage we mirror the usage of Behrensmeyer *et al.*, 1997). The  $C_2$  value and number of localities are strongly positively correlated (as would be expected if the index measures sampling adequacy in some sense). It can also be noted that the time slice 2.7–2.4 Mya is better sampled than expected for its number of localities, while the time slice 1.5–1.2 Mya is more poorly sampled. This issue is worth keeping in mind in the results and discussion.

Mean standing richness is weakly correlated with sampling completeness (Fig. 3C). It is important to note that this correlation is lower than between mean standing richness and number of localities in each



**Figure 3.** Quality assessment of the data. A, diagram of completeness values [ $C_1 = (N_{\text{tot}} / (N_{\text{tot}} + N_{\text{rt}})) * 100$  and  $C_2 = (N_{\text{bda}} / (N_{\text{bda}} + N_{\text{rt}})) * 100$ ] for 300-kyr bins from 4.2 to 0.9 Mya. The 85% cutoff line is arbitrarily selected, but represents a more stringent criterion than that used by Maas *et al.* (1995), who pioneered the use of these indices. All time slices from 3.6 to 1.5 Mya pass the 85% criterion for the more stringent  $C_2$  index, while for the less stringent  $C_1$  index, all time slices from 3.9 to 1.2 Mya pass. See text for fuller exposition. B, regression of the  $C_2$  completeness index against number of localities sampled in each time slice. The regression is significant (adjusted multiple  $R^2 = 0.596^{**}$ ) indicating that completeness and hence sampling adequacy increases with the number of localities sampled. C, regression of the  $C_2$  completeness index against mean standing richness in each time slice. The regression is weakly significant (adjusted multiple  $R^2 = 0.397^*$ ) indicating that completeness increases with increasing richness.

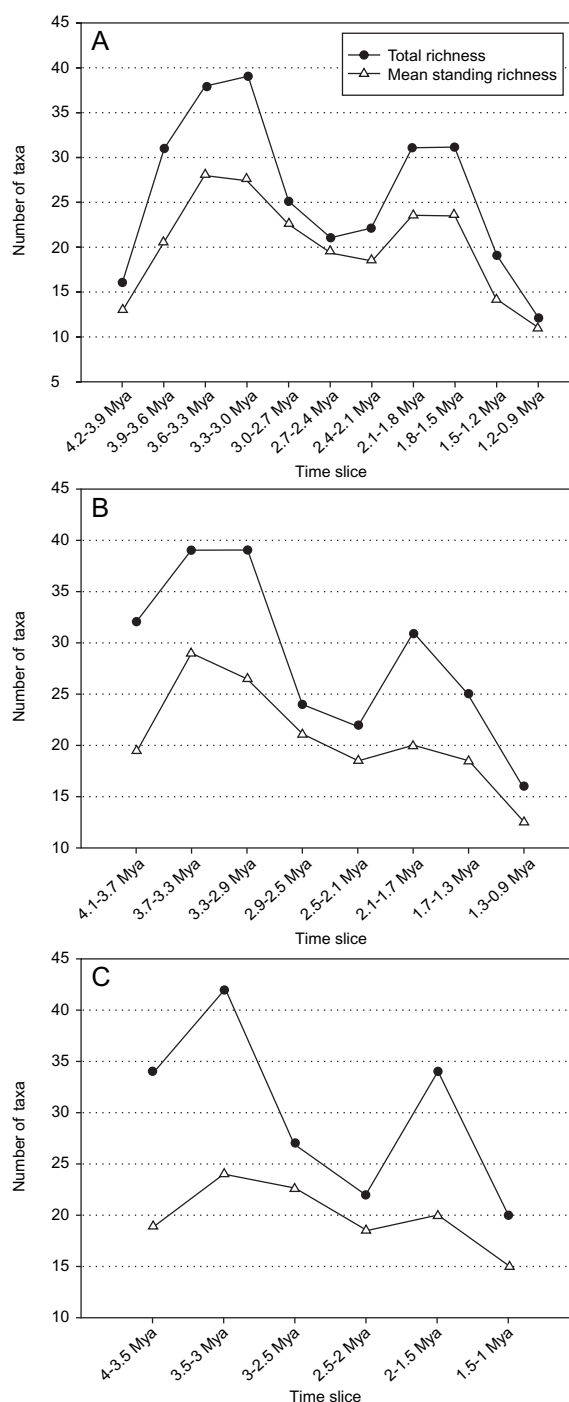
time slice (see below). It is noteworthy that time slice 2.7–2.4 Mya, which is critical for the interpretations of the data relative to the turnover-pulse hypothesis, has a lower than expected richness given its high  $C_2$ -value.

Increasing the bin size reduces the number of range-through taxa, so there is no point in showing analogous calculations for 400-kyr and 500-kyr bin sizes. The 300-kyr bin size represents the worst-case scenario for sampling adequacy, as longer bins necessarily include more material. We conclude that to the extent that the completeness indices of Maas *et al.* (1995) actually measure data quality, the present data are sufficiently adequate to be used in the following analyses without entirely biasing the results.

#### SPECIES RICHNESS

Figure 4A shows the species richness of Carnivora in eastern Africa in 300-kyr bins from 4.2 to 0.9 Mya. The record after about 0.9 Mya is too poor to be useful here (and even the 1.2–0.9 Mya time slice has a relatively low  $C_2$  value, cf. Fig. 3A). The figure shows both total species counts (i.e.  $N_{FL} + N_{bL} + N_{Ft} + N_{bt}$  in the terminology of Foote, 2000) and mean standing richness, calculated as  $(N_{bL} + 2N_{bt} + N_{Ft})/2$ . At present there are 36 species of Carnivora in the region studied, including the herpestids *Bdeogale*, *Dologale* and *Rhynchogale* and the nandiniid *Nandinia*. These latter four genera today have a limited distribution in the region and likely never occurred in the areas and habitats sampled in the fossil record.

Figure 4A shows that, based on total counts, there are two peaks in species richness of Carnivora in eastern Africa during the Plio-Pleistocene. The first is in the interval 3.6–3.0 Mya, with a maximum of 39 species in the 3.3–3.0 Mya interval. The second peak is in the interval 2.1–1.5 Mya, where the maximum at 2.1–1.5 Mya is 31 species. In the interval 3.0–2.1 Mya, species richness dips, with a minimum at 2.7–2.4 Mya of 21 species. The total counts data thus suggest that there is a sharp dip in species richness at 3 Mya and an almost equally sharp rise at 2.1 Mya. This result is somewhat modified by the mean standing richness calculation shown in Figure 4A. This curve suggests that there was indeed a peak in richness at 3.6–3.3 Mya, but that there was subsequently a steady decline in standing richness until 2.1 Mya, followed by a moderate increase. Of the earlier time periods, the interval 3.9–3.6 Mya includes a fairly good sample, but the period before that is clearly undersampled, which is also evident from Figure 3A. Of the later intervals, there are relatively good data from the 1.5–1.2 Mya interval, while the last, 1.2–0.9 Mya, is undersampled. Summarizing these data, there was a peak in carnivoran species richness in eastern Africa around 3.6–3.0 Mya and this richness has essentially



**Figure 4.** Richness data for Plio-Pleistocene Carnivora of eastern Africa. A, total richness and mean standing richness [ $MSR = (N_{bL} + 2N_{bt} + N_{Ft})/2$ ] in 300-kyr bins from 4.2 to 0.9 Mya. It should be remembered that the intervals 4.2–3.6 Mya and 1.5–0.9 Mya are less well sampled than the intermediate interval (cf. Fig. 3A). Peaks before 3 Mya (higher) and after 2 Mya (lower) are evident. See text for complete discussion. B, the same for 400-kyr bins from 4.1 to 0.9 Mya. Note the reduction in height of the post-2 Mya peak. C, the same for 500-kyr bins from 4.0 to 1.0 Mya.

been declining ever since, with a brief break around 2.1–1.5 Mya. This conclusion is strengthened by the realization that the majority of species originations leading to the peak at 2.1–1.5 Mya are species that are known exclusively or nearly exclusively from Olduvai, Bed I (1.87–1.7 Mya), suggesting that this peak is at least in part a sampling artefact. A richness pattern with a single peak as far back as c. 3.5 Mya and a steady decline since that time is difficult to reconcile with any model of environmental change that involves abrupt alterations or pulses.

Binning the data into 400-kyr bins (Fig. 4B) provides a very similar picture, with an absolute richness peak at 3.7–2.9 Mya with 39 species, a subsequent dip to 22 species at 2.5–2.1 Mya and a second, lower peak of 31 species at 2.1–1.7 Mya (this interval incorporates all of Olduvai, Bed I). The mean standing richness calculation again suggests a peak in richness at around 3.5 Mya (3.7–3.3 Mya interval) and a subsequent, gradual reduction in diversity until the quality of the record is sharply reduced at about 1 Mya.

Binning the data into 500-kyr bins (Fig. 4C) again results in a very similar pattern. In this case, the main peaks are at 3.5–3 Mya (42 species) and 2.0–1.5 Mya (34 species), with a sharp dip in between, at 2.5–2.0 Mya (22 species). Interestingly, the mean standing richness calculation leads to a clear richness peak from 3.5 to 3.0 Mya, with a more or less gradual decline in standing species richness since that time.

The species richness of Carnivora in eastern Africa in the Plio-Pleistocene can thus be summarized as starting at a low level after the Miocene–Pliocene boundary (though how low cannot be determined due to the limited sampling of the earliest Pliocene), peaking somewhere around 3.5 Mya, and subsequently declining slowly but steadily as far as the record can be followed. The latter part (last 2 Myr) of this record matches that of Behrensmeyer *et al.* (1997) in the gradual decline in overall species richness. However, the peak in carnivoran richness comes earlier than in any previous compilations in this time period and geographical region. There is no indication in the richness data of a turnover pulse anywhere between 3 and 2 Mya.

### TURNOVER

What are the underlying turnover patterns that have led to the species richness pattern described above? To investigate this question, we calculated both per-taxon and per-capita rates of origination and extinction (Foote, 2000). The former is calculated as  $(N_{FL} + N_{FT})/N_{tot}/\Delta t$  (originations) and  $(N_{FL} + N_{BL})/N_{tot}/\Delta t$  (extinctions), where  $N_{tot}$  is total richness as discussed above and  $\Delta t$  is interval length. Because interval lengths in the present case all are the same, this term can be

ignored. Per capita rates of origination ( $p$ ) and extinction ( $q$ ) per lineage million years (Raup, 1985) are estimated by Foote (2000) as  $p = -\ln(N_{bt}/N_t)/\Delta t$  and  $q = -\ln(N_{bt}/N_b)/\Delta t$ , where  $N_t = N_{FT} + N_{bt}$  and  $N_b = N_{BL} + N_{bt}$ . Despite the more intuitive appearance of the per-taxon metric, the per-capita one has a number of desirable properties, as discussed by Foote (2000), and we will favour these calculations in the following discussion. The differences between per-taxon and per-capita rates are slight, however, and both are presented in Figures 5 and 6.

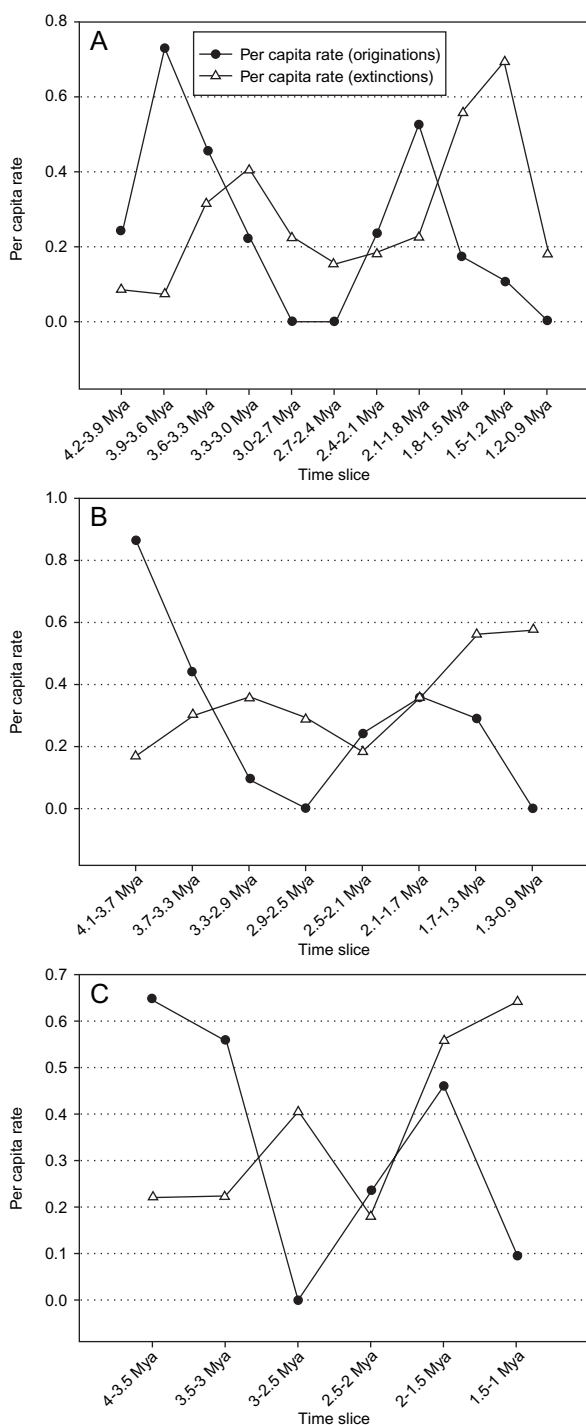
Figure 5A shows per-capita origination and extinction rates for 300-kyr bins. There are two major origination peaks, at 3.9–3.6 Mya and at 2.1–1.8 Mya. Both of these must to some extent be considered artefacts, as the former is influenced by the poor sampling of the earliest Pliocene and the presence of the species-rich Laetoli locality, and the latter by the appearance of a number of taxa specific to Olduvai, Bed I. Nevertheless, it is clear that there are peaks of origination before 3.0 Mya and after 2.4 Mya. Origination rates are, however, zero from 3.0 to 2.4 Mya. We emphasize that this rate is not just lower than in the preceding and following intervals: there are, in fact, no originations at all among Carnivora in the 3.0–2.7 and 2.7–2.4 Mya bins. Comparison of the origination rates with the richness pattern (Fig. 4A) shows that the moderate peaks in richness at 3.3–3.0 Mya and 2.1–1.5 Mya can be directly related to the peaks in the origination rate curve.

The extinction rate curve in Figure 5A is different from the origination curve in several respects. The early peak is much lower and the later one much higher; they are shifted towards the recent (as would be expected, since an increase in extinction rate usually follows an increase in origination rate) and the extinction rate is never zero. The overall impression is of a fairly constant extinction rate of between 0.2 and 0.4, which increases dramatically after 1.8 Mya.

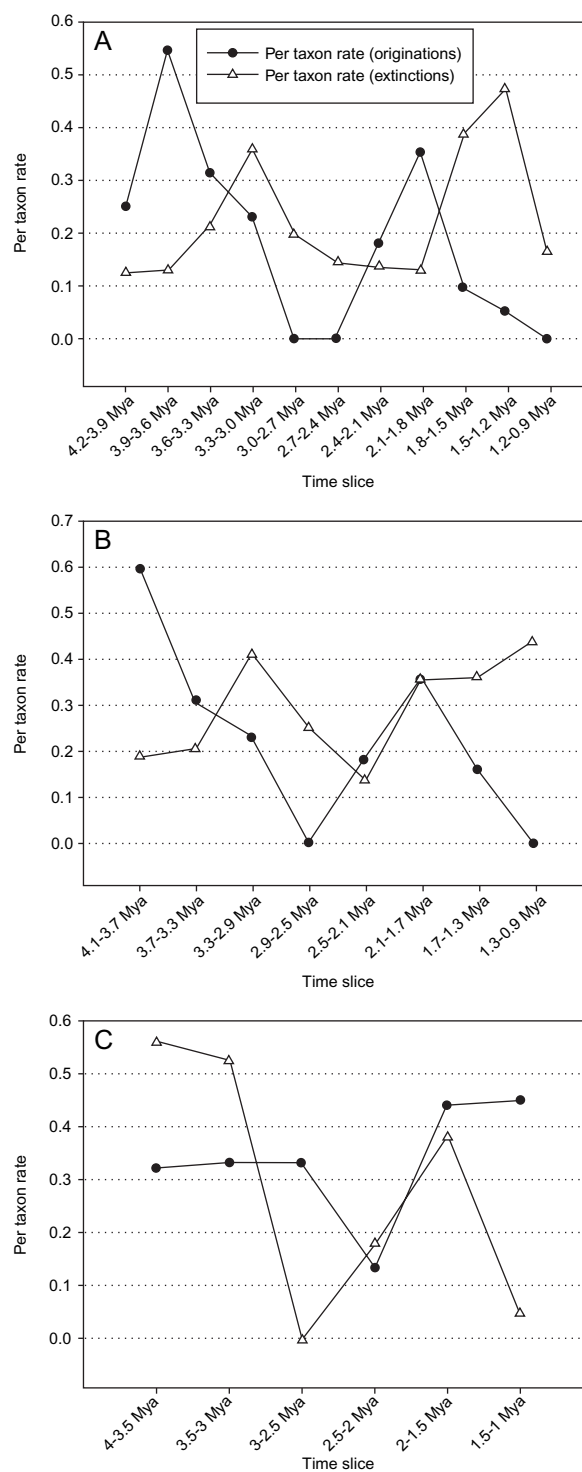
What is perhaps most significant about the origination and extinction rate curves in Figure 5A is that in the interval 4.2–3.3 Mya, the rate of origination exceeds the rate of extinction. After 3.3 Mya, extinction rate exceeds origination rate, except for the 2.4–1.8 Mya interval. The latter excess of originations may, again, to some extent be an artefact of the presence at Olduvai of several endemic species.

In Figure 5B and C the per-capita origination and extinction rates are shown for 400-kyr and 500-kyr bins, respectively. The patterns observed are identical to those seen in Figure 5A for the 300-kyr bins. This demonstrates that the patterns are unlikely to be artefacts of the binning.

In Figure 6A–C we present the per-taxon origination and extinction rate calculations for 300-kyr, 400-kyr, and 500-kyr bins. The results are the same as for



**Figure 5.** Per-capita rates of origination and extinction for Plio-Pleistocene Carnivora of eastern Africa. A, 300-kyr bins from 4.2 to 0.9 Mya. It should be remembered that the intervals 4.2–3.6 Mya and 1.5–0.9 Mya are less well sampled than the intermediate interval (cf. Fig. 3A). Note especially the zero origination rate in the interval 3.0–2.4 Mya. See text for complete discussion. B, the same for 400-kyr bins from 4.1 to 0.9 Mya. C, the same for 500-kyr bins from 4.0 to 1.0 Mya.



**Figure 6.** Per-taxon rates of origination and extinction for Plio-Pleistocene Carnivora of eastern Africa. A, 300-kyr bins. B, 400-kyr bins. C, 500-kyr bins. The diagrams match those for per-capita rates closely, demonstrating that the results are not dependent on the exact metric used.



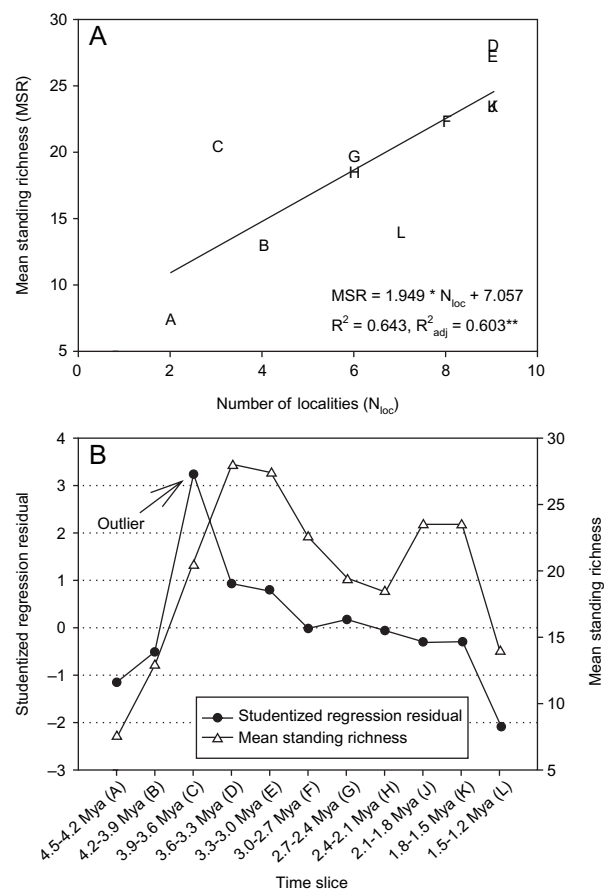
the per-capita rates in every respect. Originations still show an early and a late peak with a drop to zero in between, while extinctions show a steady pattern ending in a late peak. This demonstrates that the patterns observed are unlikely to be an artefact of the calculation method.

In summary, the origination and extinction rate curves give no indication of a turnover pulse around 2.5 Mya. Indeed, there is almost no turnover at all among the Carnivora at that time and more specifically, no originations. It might be argued with Turner (1999) that Carnivora would be expected to lag behind their prey species in turnover pattern. However, leaving aside the problem of actually justifying this expectation theoretically, in practice the problem of relating a specific turnover pulse among Carnivora to a particular environmental or climatic event becomes nearly insurmountable. How much time should we allow to pass and still be able to claim that the former was caused by the latter? At this stage, we prefer to take the data literally and feel that there is nothing in our richness or turnover data to support the presence of a turnover pulse among the carnivorans of eastern Africa around 2.5 Mya.

#### BIASES

Some additional aspects of bias in the record can be studied by analysing the relationship between number of localities and the mean standing richness in each time slice. This analysis is shown for 300-kyr bins in Figure 7 and for 400-kyr and 500-kyr bins respectively in Figures 8 and 9. Not surprisingly, there is a correlation between these two measures. The analysis of sampling adequacy discussed above indicated that the faunas are reasonably well sampled. It may thus be hypothesized that rather than indicating more taxa with greater sampling intensity, the correlation in Figure 7A instead indicates that more localities increases the number of different habitats sampled and thus the gamma- rather than the alpha-diversity observed in the material. However, this possibility should be viewed in relation to the residual of the regression of Figure 7A. This residual is shown for each time slice in Figure 7B. The pattern of residuals is interesting as time slices with low completeness (A, B, and L; Figs 3A and 7A) have negative residuals on the regression (i.e. lower than expected richness), which perfectly matches expectations.

On the other hand, time slice 3.6–3.3 Mya has a high positive residual and thus a higher than expected mean standing richness for the number of localities sampled in that time slice. This clearly shows the effect of Laetoli (completely dominant in this time slice) on the early parts of the record. Despite this, however, the time slice 3.3–3.0 Mya retains high rich-

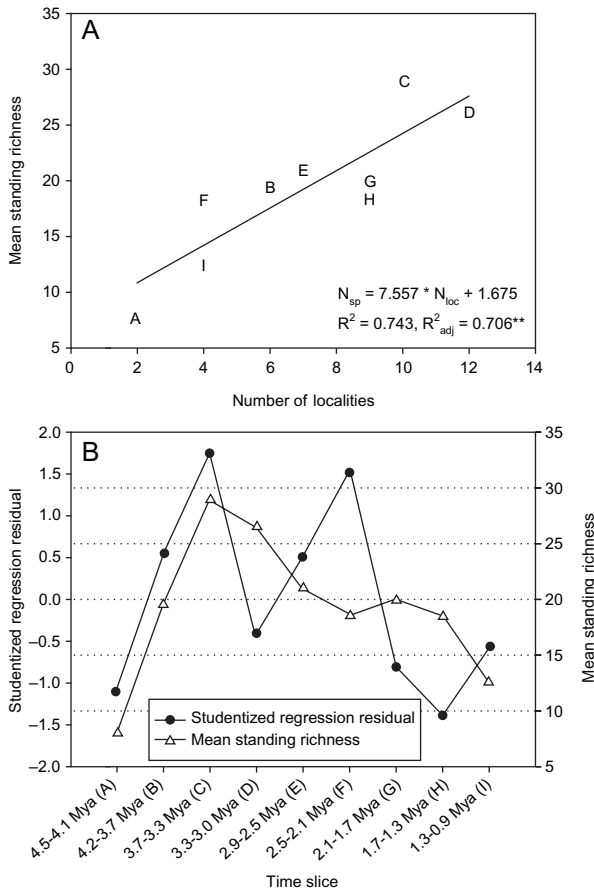


**Figure 7.** Results of the regression analysis of number of localities vs. mean standing richness for 300-kyr bins. A, regression analysis. The correlation is significant (adjusted multiple  $R^2 = 0.603^{**}$ ). Note that time slice C (3.9–3.6 Mya) is an outlier. B, regression residuals plotted against time slice showing the high positive residual for the outlier, time slice C, indicating that this time slice has more taxa than expected given the number of localities present, which is probably an effect of the dominance of the species-rich Laetoli locality in this time slice. Laetoli also has an effect in time slice D (3.6–3.3 Mya), but this time slice includes many more localities and therefore the effect of Laetoli is not as evident.

ness (both mean standing richness and raw species counts, cf. Fig. 4A), indicating that Laetoli is not solely responsible for the high richness peak prior to 3 Mya. No similar effect of a single locality is seen for the second richness peak, 2.1–1.5 Mya, despite the presence during these time slices of a number of species only found at Olduvai.

In summary, there are many potential biases in a record with a relatively small number of specimens per taxon. However, sampling completeness appears fairly good and some other biases, such as poor sampling in the early and late parts of the record and





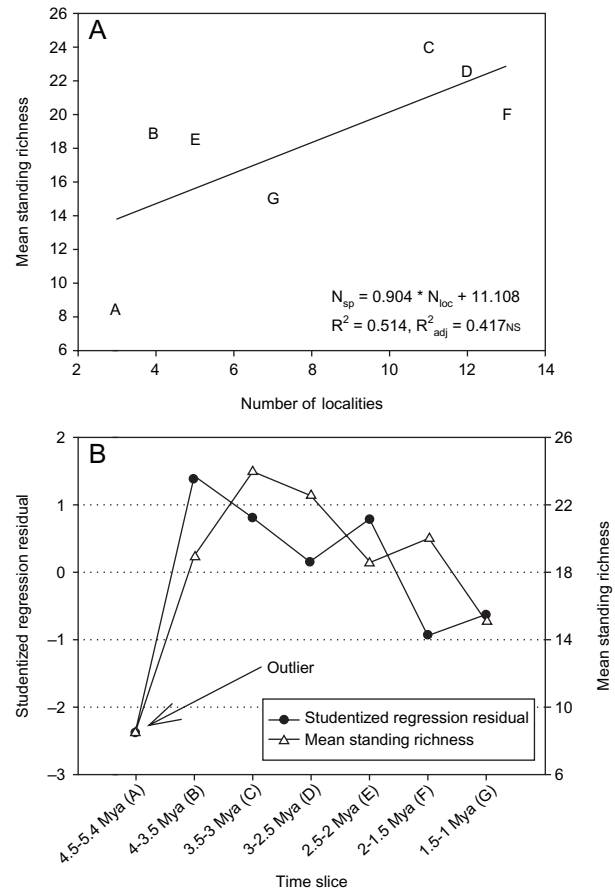
**Figure 8.** Results of the regression analysis of number of localities vs. mean standing richness for 400-kyr bins. A, regression analysis. The correlation is significant (adjusted multiple  $R^2 = 0.706^{**}$ ). There are no statistical outliers in this regression. B, regression residuals plotted against time slice. There are no outliers, but the effect of Laetoli is still seen in the relatively high residual for time slice C (3.7–3.3 Mya).

undue influence of Laetoli on some time slices are readily identifiable and therefore possible to control for. We interpret the correlation between number of localities and mean standing richness as reflecting a sampling of more disparate habitats rather than a lack of sampling effort in general. Habitat heterogeneity and concomitant changes in beta-diversity across time in eastern Africa represent an interesting avenue of research, but this is beyond the scope of the present contribution.

## DISCUSSION

### ORIGIN OF THE MODERN FAUNA

It may be appropriate to start this discussion with a few words about the modern fauna and its develop-



**Figure 9.** Results of the regression analysis of number of localities vs. mean standing richness for 500-kyr bins. A, regression analysis. The correlation is not significant (adjusted multiple  $R^2 = 0.417$  NS). Note that time slice A (4.5–4 Mya) is an outlier. B, regression residuals plotted against time slice showing the high negative residual for the outlier time slice A. The effect of Laetoli in time slice B (4–3.5 Mya) is hardly noticeable.

ment. One of the most striking aspects of our data is that so few of the living species have a definite fossil record in eastern Africa. Of the larger Carnivora only three species, *Panthera leo*, *P. pardus* and *Hyaena hyaena*, have a definite record that extends beyond the last half-million years. In all three cases, the well-established record goes back to about 1.9 Mya, while for both of the felids the possible record goes back to Laetoli, i.e. to before 3.5 Mya. Among the smaller Carnivora, the four species with a fossil record are *Melivora capensis*, *Genetta genetta*, *Helogale hirtula* and *H. ichneumon*. In the case of the first and last the record goes back to Laetoli (though the distinction between *M. capensis* and *M. benfieldi* is not always clear), while *H. hirtula* is known from about 2.5 Mya and *G. genetta* from about 2 Mya. A fifth taxon, *Ichneumia albicauda*, has a tenuous record from Olduvai.

Among the Canidae, *Otocyon megalotis* has a precursor at c. 1.9–1.7 Mya, while one or more species of jackal is known up to c. 1.3 Mya. This suggests (but of course it does not prove) that the modern taxa appeared in eastern Africa after these dates. Furthermore, indications from other regions (Lewis & Berger, 1998; Stiner *et al.*, 2001) are that *Canis pictus* evolved within the last million years. The same is true of the spotted hyena, *Crocota crocuta*, which on present evidence must have evolved after 1 Mya, and perhaps considerably later. There is material that is closely similar morphologically to each of the smaller cats, except *Profelis aurata*, and may be conspecific with them. These records go back to Kanapoi and Laetoli.

Hence, among the larger carnivorans, a few modern species may have first appearances in eastern Africa in the middle Pliocene, while others appeared there as late as within the last million years, and in some cases probably substantially less. The situation is more or less analogous among the smaller carnivorans, although there are many species in this group that have no reasonably close relatives in the eastern African fossil record, and it thus becomes impossible to judge their time of appearance in the region.

#### TURNOVER PATTERNS

As demonstrated above, the turnover pattern in eastern African carnivorans is the opposite of that which one would expect under the prevailing form of the turnover–pulse hypothesis, if the pulse occurred with the change in dominant climatic cycle at c. 2.8 Mya or so (deMenocal & Bloemendal, 1995; Vrba, 1995; Turner, 1999). This could, of course, mean a number of things. It could mean that the hypothesis is wrong, but that would be taking the question beyond the scope of the data presented here, which can at best be considered a small part of the overall picture. Alternatively it could also mean that the hypothesis is wrong for carnivorans, whatever its validity for other groups of mammals. This possibility can be tackled in two ways. One can look at the pattern in other groups of mammals to see whether this is congruent with the carnivoran pattern, or one can try to develop a theoretical framework for studying how turnover pulses triggered by climatic change would affect mammals at different trophic levels. It is inarguable that carnivores would be less affected than herbivores by a climatic change that had a primary effect on the vegetation (Turner, 1999), but it would be too easy to assume that the effect would simply be delayed. If carnivores differ from other mammalian groups in this respect, it may be in unpredictable ways, for which new theories must be developed. It appears, for example, that carnivorans were the mammalian group hardest hit by the Messinian event that terminated the Miocene

(Werdelin & Turner, 1996; Werdelin, 1996a,b), but as yet we do not understand why this should be the case.

A recent study (Behrensmeyer *et al.*, 1997) of turnover in the Turkana Basin yielded results that are partly congruent with ours. This study had few localities older than 3.5 Myr, so results before that time cannot be compared. It included few carnivorans, and from that perspective the data can be considered independent. In the interval 3–2 Mya, Behrensmeyer *et al.*, (1997) found a gradual increase in diversity, followed by a reduction in diversity after 2 Mya. In our study we found an overall reduction in diversity from about 3.3 Mya onwards. However, the pattern of origination and extinction rates is similar, with origination rates being greater in earlier parts of the record and a dominance of extinction rates in the later part. Neither study found evidence of a turnover pulse in the 3–2 Mya interval. We find a reduction in turnover during that time, while Behrensmeyer *et al.* (1997) found a gradual increase in turnover.

What does the record actually tell us? Combined with other knowledge, particularly of carnivorans from other regions, such as southern Africa and Eurasia, it suggests the following. There was an extinction event in the carnivoran record near the Miocene–Pliocene boundary, just as in Eurasia (Werdelin & Turner, 1996; Werdelin, 1996a, b), but perhaps slightly later in time, to judge from the persistence at Langebaanweg, South Africa (earliest Pliocene) of some typically Miocene forms. The early peak in origination rate, while in part an artefact of a poor early record, reflects the beginning of the bounce-back from the Mio-Pliocene extinction event. This bounce-back was triggered initially by local diversification of groups such as Hyaenidae (*Parahyaena*, *Crocota*), Felidae (*Dinofelis*, *Homotherium*) and Mustelidae (*Enhydriodon*, *Torolutra*). Laetoli may be the latest expression of this diversification, with material of taxa not known from other sites.

The later stages of the early high turnover interval are characterized by a dispersal event into eastern Africa of taxa such as *Canis*, *Megantereon* and small mustelids (presumably from the north) and *Hyaena* (from the south).

After this dispersal event, turnover among carnivorans in eastern Africa takes on a new character, with higher extinction than origination rates. The underlying cause of the gradual but persistent decline in species richness of Carnivora after c. 3.3 Mya is not entirely clear, but we hypothesize (and hope in the future to test) that what we are observing is a gradual extinction of habitat and prey specialists (such as sea otters and sabretooths) and a survival of generalist carnivorans (such as dogs and pantherine cats). For carnivorans, the last million years has been the age of the generalist.

## CONCLUSIONS

Work in this area is only beginning and a number of ways of improving the data and analyses are evident. A better taxonomic database is obviously a prerequisite and our work is directed towards this end. From a theoretical perspective, this work would be enhanced by a better understanding of the different responses to environmental change exhibited by animals at different trophic levels. Currently, the best we can do is to say that a hypothesized turnover pulse in carnivores should come 'later' than one in herbivores. However, it is not obvious that turnover pulses in herbivores and carnivores should be coupled at all, and even if they are, more precise boundaries on the term 'later' are needed. As it is, we are left with the result that turnover in Plio-Pleistocene Carnivora of eastern Africa does not support the idea of a turnover pulse between 3 and 2 Mya. On the other hand, the carnivoran data are also not entirely congruent with turnover data on herbivores from the Turkana Basin.

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