

KIRTLANDIA

The Cleveland Museum of Natural History

December 2007

Number 56:121–139

CARNIVORA (MAMMALIA) FROM LEMUDONG'O (LATE MIOCENE: NAROK DISTRICT, KENYA)

F. CLARK HOWELL

Human Evolution Research Center, Museum of Vertebrate Zoology
University of California, Berkeley, California 94720-3160

AND NURIA GARCÍA

Human Evolution Research Center, Museum of Vertebrate Zoology
University of California, Berkeley, California 94720-3160
Dpt. Paleontología, Universidad Complutense Madrid, F.C.
Geológicas
Ciudad Universitaria, s/n, 28040, Madrid, Spain
Centro (UCM-ISCI) de Evolución y Comportamiento
Humanos, C/ Sinesio Delgado 4, Pabellón 14, 28029, Madrid, Spain
ngarcia@isciii.es

ABSTRACT

Lemudong'o, a fossiliferous locality in Narok district (Kenya), adjacent to the southern reaches of the Kenya Rift Valley, yields vertebrates in the still poorly-known span of the African late Miocene. The associated isotopic age is ~6.1 Ma, correlative with well-known local faunas of western Eurasia assigned to the final Turolian or MN-13 (Mammal Neogene-Zone). This local fauna comprises Canidae (1 species), Felidae (2 species), Viverridae (2 species), Herpestidae (at least 4 species), Hyaenidae (1 species), Mustelidae (1 species), and Procyonidae (1 species). The assemblage both confirms and amplifies the overall composition of such mammal fauna from other African localities of comparable, or rather younger or older age(s), and enhances the basis for comparison with well-known counterparts of western Eurasia.

Introduction

The Lemudong'o locality is of particular interest and importance due to the demonstrable uppermost Miocene age of the attendant sedimentary sequence (Ambrose et al., 2003; Deino and Ambrose, 2007). The lowermost exposed sediments are of ≥ 6.1 Ma ($^{39}\text{Ar}/^{39}\text{Ar}$ [SCLF]) age, and the several fossil-bearing horizons, exposed at Locality 1, are of comparable or just slightly younger (6.04 Ma) age. This age is within the span of MN-13 (Mammal Neogene-Zone), the last of the tripartite Turolian-ELMMZ (European Land Mammal Megazone) of the circum-Mediterranean/western Eurasian realm (Mein, 1999; Steininger, 1999). Hence, it is broadly correlative in age with many classic fossil localities from western Asia to the Iberian Peninsula. Thus, we have one of those still uncommon African occurrences of the late Cenozoic, affording some most welcome insight into the natural world of the end-Miocene in a near equatorial setting.

Among the fossil assemblages from Lemudong'o is a sample of the often poorly represented order Carnivora. The available sample of Carnivora species is generally both fragmentary and of limited diversity in light of expectations for a local fauna of this

uppermost Miocene age. Nonetheless, it is both interesting and important as it affords some representation of Canidae, Mustelidae, Procyonidae, Viverridae, Herpestidae, Hyaenidae, and among Felidae, both Machairodontinae and Felinae.

Abbreviations

KNM Kenya National Museum.
NK Narok District indicates fossils that are from localities within this district, including Lemudong'o Localities 1 and 2, Enamankeon Localities 1, 2, and 3, and Kasioli Localities 1.

Dental abbreviations follow the convention of upper case letters = maxillary teeth, lower case letters = mandibular teeth.

Systematic Paleontology

Class MAMMALIA Linnaeus, 1758

Order CARNIVORA Bowdich, 1821

Infraorder CYNOIDEA Flower, 1869

Family CANIDAE Gray, 1821

Subfamily CANINAE Fischer von Waldheim, 1817



Figure 1. *Eucyon* aff. *intrepidus* (KNM-NK 41284), right M1 in occlusal view. Scale bar = 1 cm.

Genus *EUCYON* Tedford and Qiu, 1996

EUCYON aff. *INTREPIDUS* Morales, Pickford and Soria, 2005

Figure 1

Description and remarks

A small canid, here considered to be of the tribe Canini, is represented by elements of upper and lower dentition. KNM-NK 41053 consists of a left P1 with root. This element is readily identified as a P1 of a small canid. Its dimensions (Table 1) and simple morphology are compatible with homologs attributed to genus *Eucyon*.

KNM-NK 41284 is a right M1, lacking a root. A well-preserved upper molar crown, scarcely worn, is demonstrably canine (Figure 1). A distinction among some canids, even *Eucyon* and *Vulpes*, with relatively complete material is not always readily effected. To an extent, this is similarly the case in respect to the raccoon-dog *Nyctereutes*, several species of which are now well documented in the Pliocene of Eurasia.

Specimen KNM-NK 41284 replicates most particularly the morphology and size of its homolog in samples now attributed to the genus *Eucyon* (Tedford and Qiu, 1996). A comparison of M1 crown dimensions in such samples and KNM-NK 41284 is set out in Table 2; characters are set out in Table 3. Comparison is effected diversely with the holotype of *E. (ex-Canis) davisii* (UCMP-545), associated M1–M2 from Rattlesnake Creek (Oregon) (Merriam, 1911a, b) and associated cranio-dental material from Little Valley and from Juniper Creek Canyon (Oregon), described and figured by Shotwell (1970), from Hemphillian age faunas of the John Day region, Oregon. A newly recognized species, *E. intrepidus*, from the Lukeino Formation, Baringo, Kenya (Morales et al., 2005, p. 48) is the first nominate species of *Eucyon* from Africa.

KNM-NK 41285 consists of a left m1, preserving a posterior root, and lacking the mesio-lingual (paraconid or pad) portion of the trigonid. This small carnassial is comparable in size to some homologs attributed to *Eucyon davisii*, e.g., the UO-26742 individual, comprising associated upper and lower jaws with dentition (and postcranials) (Shotwell, 1970). Although incomplete, it is well preserved and shows scant wear. The protoconid (pr^d) is salient with the usual steep, sub-vertical distal slope to the talonid. There is a distinct but low buccal cingulum at the base of the protoconid. The metaconid (med) is distinct, enlarged and disto-lingually offset from the back of the protoconid with which it is joined by a low, salient crest. The talonid is elongate and bears marginally both hypoconid (hy^d), the larger and more posterior, and entoconid (en^d) subequal cusps, the latter a bit more distally set. There is no linkage between these cusps similar to *E. davisii*. Sometimes it may bear accessory cusplets adjacent anteriorly to hy^d and/or en^d (Shotwell, 1970). On KNM-NK 41825 there is only

Table 1. Anterior (P1) premolar dimensions (mm) in some *Eucyon davisii* and other *Eucyon* samples. North American and Odessa samples after Rook (1993); *E. minor* after Tedford and Qiu (1996).

	P1	
	length	breadth
Lemudong'o (Narok, Kenya) KNM-NK 41053	4.7	3.15
Little Valley (Ore) UO-26742	5.8	3.4
BirdBone Q (Az) F: AM-63019	5.1	3.3
F: AM-63034	4.8	2.8
Edson LF (KS) F: AM-49464	5.0	3.1
Renfro Pit (TX) F: AM-61981	4.8	2.9
Old Cabin Q (AZ) F: AM-72661	4.8	2.8
Odessa (UKR) (<i>E. odessanus</i>) n = 4	6.1 (5.9–6.3)	3.45 (3.3–3.9)
China (<i>E. minor</i>) n = 8	5.675 (4.9–6.4)	2.86 (3.0–4.0)

a small marginal beadlike elevation anterior to the entoconid. The posterior-most part of the talonid basin is simple and constricted by the aforesaid cusps. The lingual outline of the talonid is slightly convex and the buccal outline is incurved between the pr^d and hy^d. This dental element is still unknown in *E. intrepidus*.

Tedford and Qiu (1996) assigned abundant material from elsewhere in western and central North America, represented in various museum collections, as well as from the Mio-Pliocene of Asia, to the new genus *Eucyon*. It was considered by them, as well as by Berta (1988), as a stem-taxon for *Canis*-group species as well as for a set of South American canid genera. The earliest documented appearance of the genus is in the (late) middle Miocene (Clarendonian) of North America; but, it is most commonly represented there in subsequent Hemphillian local faunas. *Eucyon davisii* appears in (earlier) Pliocene Age local faunas in China, along with a larger, derived species, *E. zhoui*. The arrival of *Eucyon* into western Eurasia is documented in the latest Miocene (late Turolian, MN-13) of Brisighella (Italy) by a derived *Canis* species, among the oldest such known in Europe (Rook et al., 1991, p. 19). It was initially attributed to "*C.*" *monticinensis* (Rook, 1992, p. 152), and only subsequently transferred to *Eucyon* (Rook, 1993, p. 25). The same, or related, species is recorded from Alatini (Macedonia, Greece), represented by a mandible, once (and originally) referred to *Nyctereutes donnezani* (Sickenberg, 1972, p. 501–503) and known now to derive from a Ruscinian (lower Pliocene) context (Koufos, 1997, p. 43). A canid sample from the Ruscinian-age karstic infillings ('catacombs') of Odessa (Ukraine), assigned to *Vulpes odessana* (Odintzov, 1967, p. 130), is also now attributed to *Eucyon* (Tedford and Qiu, 1996). However, a still older canine (MN-12 attribution) in Western Europe is, perhaps, *Canis cipio* (Crusafont, 1950, p. 45–47; Pons and Crusafont, 1978), first documented at Conclud (or Cerro de la Garita) (maxilla with P4-M2) and subsequently at Los Mansuetos (an m1), Teruel basin, Spain (Alcala, 1994).

The African record of the Mio-Pliocene Canidae is still scant. Langebaanweg has yielded cranio-dental remains perhaps representative of *Eucyon* (Hendey, 1974; Rook, 1993). Younger, about mid-Pliocene age, occurrences of several canid taxa, including *Canis* sp., are reported from Laetoli (Tanzania) (Barry, 1987) and from south Turkwell (Turkana, northern Kenya) (Werdelin and Lewis, 2000).

In the latter instance, gnathic and several postcranial parts definitely attest to the genus *Canis* (*Canis* sp. nov. A of the authors, p. 1176) at 3.5 Ma. In the former instance incomplete cranio-dental and various postcranial remains, attributed to aff.

Table 2. Upper molar (M1) dimensions (mm) in some samples of *Eucyon* species and in KNM-NK 41284. *E. intrepidus* after Morales et al. (2005), *E. davisi* after Rook (1993), *E. monticiniensis* after Rook (1992), *E. odessanus* after Rook (1993), *E. minor* after Tedford and Qiu (1996), cf. *Eucyon* Langebaanweg (after Hendey, 1976; Rook, 1993) and *C. cipio* after Crusafont (1950).

	M1	
	length	breadth
Lemudong'o (Narok, Kenya) KNM-NK 41284	8.06	11.6
Lukeino Fm. (Baringo, Kenya) BAR 2127 '01 (<i>E. intrepidus</i>)	9.3	11.0
BAR 719 '02 (<i>E. intrepidus</i>)	9.6	12.7
<i>Eucyon davisi</i>		
Rattlesnake Creek (Ore) UCMP-545	10.0	11.6
Thousand Creek (Ore) UO-12505	10.1	12.7
Little Valley (Ore) UO-26742	11.2	13.7
Bird Bone Q (AZ) <i>n</i> = 13	11.08 (10.0–12.5)	13.2 (11.3–15.7)
Clay Banc Q (AZ) <i>n</i> = 4	11.05 (10.9–11.05)	12.85 (12.4–13.4)
Edson LF (KS) <i>n</i> = 1	8.9	12.0
Optima LF (OK) <i>n</i> = 2	11.0–11.2	12.7–13.1
Miami Q (TX) <i>n</i> = 3	10.9 (10.3–11.4)	11.1 (8.0–13.2)
Old Cabin Q (AZ) <i>n</i> = 6	10.53 (9.7–11.3)	12.8 (12.0–14.0)
Monticino (Brisighella, It) <i>n</i> = 1 (<i>E. monticiniensis</i>)	12.0	13.7
Venta del Moro (Sp.) <i>n</i> = 1 (<i>E. monticiniensis</i>)	11.2	12.7
Concud (Sp.) <i>n</i> = 1 (<i>C. cipio</i>)	13.1	15.8
Odessa (Ukr.) <i>n</i> = 7 (<i>E. odessanus</i>)	11.0 (10.1–11.8)	13.0 (11.5–14.4)
China <i>n</i> = 9 (<i>E. minor</i>)	9.94 (10.0–11.8)	13.17 (12.2–13.9)
Langebaanweg <i>n</i> = 2 (cf. <i>Eucyon</i> sp.)	10.1	11.5–13.0

Canis brevirostris (Euer) by Barry (1987, p. 237–240), with a size comparable to extant *Nyctereutes*, actually exhibits features found within the morphometric range of *Eucyon* (Rook, 1993) and at substantially younger, mid-Pliocene, age than previously discussed Kenyan localities.

Infraorder ARCTOIDEA Flower, 1869
 Parvorder MUSTELIDA Tedford, 1976
 Family MUSTELIDAE Swainson, 1835
 Subfamily GULONINAE Gray, 1825
 Genus *PLESIOGULO* Zdansky, 1924

PLESIOGULO BOTORI Haile-Selassie, Hlusko, and Howell, 2004
 Figure 2

Description and remarks

The holotype, KNM-NK 41420, is a cranial fragment corresponding to a partial right temporal with glenoid cavity and teeth from both sides: right P3 (two crown fragments), P4-M1, and left P3-M1 and left M2 (belonging to the same individual) (Figure 2). KNM-NK 36518a consists of a left upper canine. KNM-NK 36518b consists of a right lower canine.

Table 3. Upper (M1) molar morphology (characters after Wang et al., 1999) in some samples of *Eucyon* species and KNM-NK 41284.

	<i>Eucyon intrepidus</i>			<i>Eucyon davisi</i> (North America)		
	KNM-NK 41284 ¹	BAR 2127'01-719'02 ³	UCMP-545 (type) ¹	UCMP-12505 ¹	UOE-26742 ²	
	Lemudong'o, Kenya	Lukeino Fm., Kenya	Rattlesnake Creek, Ore.	Thousand Creek, Nev.	Little Valley, Ore.	
Crown form	51 1a - subtriangular	1a - subtriangular	1a - subtriangular	1a - subtriangular	1 - subquadrate	
Distal border of crown	57 00 - scarcely incurved	00 - scarcely incurved	0 - slightly incurved	00 - scant incurvature	0 - slightly incurved	
Buccal cingulum...						
re paracone	50 0 - present, weak	0 - present, weak	0 - present	0 - present, broken, inc	0 - present	
re metacone	49 0 - present, stronger	0 - present, stronger	0 - present	? broken	0 - present	
Lingual cingulum	52 1 - extended anteriorly around pr	1 - extended anteriorly around pr		2 - thickened anteriorly	0 - largely set and extended linguo-distally	
Parastyle	48 2 - lost	2 - lost	2 - lost	2 - apparently lost	2 - lost	
Buccal cusps pa re me	55 1 - pa larger, higher	1 - pa larger, higher	1 - pa larger, higher	1 - pa larger, higher	1 - pa larger, higher	
Hypocone	54 3 - thickened lingual cingulum	3 - thickened lingual cingulum	0 - absent	3 - thickened lingual cingulum	2 - as broad lingual cingulum and displaced disto-lingually	
Paraconule	56 1 - distinct cusplet, on anterior loph	0/1 - semi-distinct anterior loph cusplet	1 - thickened part of anterior loph	1 - distinct cusplet, on anterior loph	0 - absent	
Metaconule	53 1 - distinct cusplet at junction anterior loph & distal cingulum	1 - distinct, enlarged cusplet	1 - thickened part of lingual-distal cingulum	1 - distinct cusplet at junction anterior loph & distal cingulum	0 - weak swelling on loph	
Protocone	distinct, enlarged m-l cingulum cusp	subangular, m-l cingular cusp	indistinct, ? thickened m-l cingulum	weak enlargement m-l cingulum	distinct, small on mesial crista	

¹ Personal observations

² After J.A. Shotwell (1970)

³ After Morales et al. (2005)



Figure 2. *Plesiogulo botori* (KNM-NK 41420), right temporal with P4 and M1 in occlusal view. Scale bar = 1 cm.

The two canines could well correspond to a different, smaller individual as they appear small compared to the large dimensions of the P3-P4-M1 of the holotype (KNM-NK 41420).

The new species of *Plesiogulo*, described elsewhere by Haile-Selassie et al. (2004a), is represented both at Lemudong'o and at the Adu Dora locality, Middle Awash (Afar depression, Ethiopia). The latter, a paratype, comprises an isolated left M1 (ADD-VP-1/10, NME). Up until the introduction of the new species, a total of about seven seemingly valid species, including synonymies, have been proposed (Kurtén, 1970). Two, *P. monspessulanus* (Asia, Europe, S. Africa) and *P. lindsayi* (N. America), are large, and five, *P. minor* (Asia), *P. crassa* (Asia, Europe), *P. brachygnathus*, and *P. praecocidens* (Asia, E. Africa), and *P. marshalli* (N. America), are smaller, even considerably so (Harrison, 1981). The first known occurrence in Africa was the recovery at Langebaanweg (South Africa) of cranial, jaw, teeth, and postcranial bones referred by Hendeby (1978a) to *P. monspessulanus*. *Plesiogulo botori* is distinguished (Table 4) on dental characteristics only (thus far) as the largest yet known species, with P3 and P4 both longer and wider, and M1 longer (than for *P. monspessulanus*), lacking an anterior cingulum on P4, a notably expanded internal lobe of M1, high protocone and discontinuous lingual cingulum of M1. Postcranial remains are not yet definitively known for *P. botori*. *Plesiogulo praecocidens*, an Asian species, has recently been recognized (by Morales et al., 2005, p. 52) from upper teeth, at localities of the Lukeino Formation (Baringo basin), Kenya.

Parvorder MUSTELIDA Tedford, 1976
 Family PROCYONIDAE Gray, 1825
 Subfamily SIMOCYONINAE Dawkins, 1868
 Genus *SIMOCYON* Wagner, 1858
SIMOCYON species indeterminate

Figure 3

Description and remarks

KNM-NK 45780 consists of a left M1/crown, complete and unworn (Figure 3). The specimen is distinguished by a sub-triangular crown, trigon basin dominated by the two buccal cusps, subconical with pointed tips and each with an anterior and posterior low descendant crest. These cusps, paracone (pa) and metacone (me), are closely appressed in their bases, though separated above by a strong fissure; the paracone (pa) is overall

larger and notably higher than the metacone (me). The salient mesial and posterior trigon crests (pre- and post-protocrista) are simple, unadorned, and are confluent curvingly at the position of the protocone (pr) that is, however, undifferentiated as a distinct cusp. The inner margin of the crown is markedly prolonged lingualward of the trigon, distinguished by its massive basal cingulum, which girds the whole lingual extent of the crown and hence affords a somewhat linguale or trapezoidal form to the crown. There is a distinct, rather weak buccal cingulum along that outer margin of the paired buccal cusps.

The single element of the upper molar dentition matches in every respect its homolog in (at least) three specimens (from Pikermi and Halmyropotamus in Europe, and from Fugu in China) representing the genus (and species) *Simocyon primigenius* (Wagner, 1858). It is at the smallest end of the known range of variation of a total of ten such molars representing this species (Table 5). It is here referred to *Simocyon* sp. indet., and constitutes, to our knowledge, the first known record of the taxon in Africa.

Simocyon is not a very common element, although it is persistent within upper Miocene faunas to which it is largely confined. It is known now from over a dozen localities, including Concud (MN-12) in Spain, Eppelsheim (MN-9, type of the species *S. diaphorus*) and Dorn-Dürkheim (MN-11) in Germany, Montredon (MN-10) in France, Csákvár (MN-11, source of the purported species, *S. hungaricus*) in Hungary, Kalimanci (MN-12) in Bulgaria, two localities in Ukraine, and three in central China, as well as those set out in Table 5 in which dimensions of M1 are given. Attributed to *S. batalleri* are specimens from Sabadell environs (type) and Bovila Sagués (or San Miguel del Taudell), both Catalonia, and the recently investigated Cerro de Batallones-1 (MN-10) locality near Madrid. It had been thought to have a strictly Eurasian distribution. However, there is definite evidence for its dispersal into western North America (Qiu, 2003), as it is documented in the late Miocene (Hemphillian) of Oregon (Rattlesnake Formation), once recognized as *Pliocyon* (Thorpe, 1921), then *Araeocyon* (Thorpe, 1922), now *S. marshi*. Subsequently, it has been recorded as well from such local faunas in southern Idaho and in Nevada (Tedrow et al., 1999). In western Eurasia it is temporally limited in occurrence in Vallesian and Turolian faunas (Ginsburg, 1999); in China it has been documented in Baodean and, later, Yushean faunas (Qiu and Qiu, 1999). Its postcranial skeleton was once apparently wholly unknown; among the recently recovered, rich carnivore assemblage of Cerro de Batallones (Madrid province, Spain), partial skeletons of *Simocyon* are represented (Peigné, Salesa, et al., 2005) and are still under study.

Even cranial remains have been uncommon, and were first known only in Europe (initially Pikermi, subsequently, Veles and Halmyropotamus). Other localities in China (Shaanxi and Shanxi) afforded further material; recently the situation has been improved by the local faunas of Fugu (Shaanxi) (Wang, 1997) and, especially, Batallones-1 (Spain) (Peigné, Salesa, et al., 2005) which afforded much welcome insight into details of both cranial and dental morphology. Since its recovery and recognition a century and half ago the systematics, affinities, and phylogenetics of *Simocyon* became a matter of considerable controversy. Altogether as many as four species (in Eurasia) and, perhaps, another in North America, have been proposed. Possibly an older, less derived species (*S. diaphorus*), with unreduced premolar dentition, is to be distinguished from another subsequent and more derived species (*S. primigenius*) with much reduced/lost

Table 4. Comparison of upper dental dimensions¹ in *Plesiogulo*.

	<i>P. botori</i> sp. nov.	<i>P. monspessulanus</i> (= major)	<i>P. brachygnathus</i> (ex- <i>Lutra brachygnatha</i>)	<i>P. crassa</i> (= minor)	<i>P. praecocidens</i>	<i>P. marshalli</i>	<i>P. lindsayi</i>	<i>G. gulo</i>
P3								
Length	14.6	13.9	no data	11	no data	11.6	13.0	10.4
Breadth	10.2	9	no data	6.9	no data	8	9.3	6.3
Length/breadth	1.43	1.54	no data	1.59	no data	1.45	1.39	1.65
P4								
Length	24.5	23.2	17.1–20.5	18.3–20.8	17.2	20.1	23.5	19.75
Breadth	16.7	15.6	11.1–14.0	12.9	10.9	13.9	17.3	11.9
Length/width	1.47	1.49		1.51		1.45	1.36	1.66
M1								
Breadth	21.2	18.6	13.8–19.4	15.8–17.8	13.8	18.2	20.0–21.5	13.9
Lingual-lobe length	15.9	15.4	12.0–16.3	13.2	12.4	15.1	13.3–15.5	8.3
Minimum length	10.1		8.4–11.7	8.4	7.8	9.1	9.7	
Max/min length	1.57	(1.54e)		1.57	1.59	1.67	1.51	(1.34e)
Width-/lingual-lobe Length	1.33	1.21		1.28	1.11	1.21	1.41	1.68
P3/P4 length	0.59	0.59	no data	0.57	no data	0.58	0.55	0.53
P3/P4 breadth	0.61	0.58	no data	0.54	no data	0.57	0.53	0.53

¹ Data for *P. monspessulanus*, *P. brachygnathus*, and *P. crassa* are from Hendey (1978b) and Alcalá et al. (1994), Zdansky (1924), and Kurtén (1970), respectively. Dimensions of *P. marshalli* and *P. lindsayi* are from Harrison (1981). Measurements of *Gulo gulo* are from Kurtén and Rausch (1959); e = estimated from published images, all reported measurements are in mm

anterior premolar dentition and altered lower carnassial (m1) crown proportions. There is now good reason to accept the validity of a third species taxon, *S. batallerii*, from Spain, previously and first recorded in Catalonia and now very well represented at Batallones (province of Madrid). An antecedent source of *Simocyon* has ultimately come to be recognized as *Alpeocyon* (ex-*Alopecodon* Viret, 1933) *leptorhynchus* (Camp and Vanderhoof, 1940), known from middle Miocene localities of MN-6 (as at Göriach, Neudorf) or MN-7/8 (La Grive–St-Alban, Oppeln) ages (Thenius, 1949; Beaumont, 1964).

The phylogenetic affinities of *Simocyon*—whether among caniniformes (Cynoidea), amphicyonids/ursids (Arctoidea), or mustelids (Mustelida)—were long debated and disputed. Major contributions toward resolution of the issue have been those of Pilgrim (1931), Thenius (1949), Schmidt-Kittler (1981), Wolsan (1993) and, recently and notably, Wang (1997); and, in respect to

molecular phylogeny among procyonids, Slattery and O'Brien (1995) in their definitive work toward resolution of ailurine, red panda (*Ailurus fulgens*) phylogenetic affinities. Among the family Procyonidae are four subfamilies, Basarisinae (Gray, 1869, p. 246), Procyoninae (Gray, 1825, p. 339), Ailurinae (Gray, 1843, xxi), and Simocyoninae (Dawkins, 1868, p. 1). The detailed morphological evidence afforded by structure of basicranium (Wang, 1997) has finally brought to resolution the procyonid character of *Simocyon* and, as well, enabled full-blown explication of craniodental anatomy and its similarities and differences with the only still extant ailurine.

Table 5. Dimensions (mm) of first upper molars (M1) among known *Simocyon* samples.

	M1 (length × breadth)
Pikermi (M.9032) ¹	15.5 × 19.0
Halmyropotamus (1967.8) ²	16.0 × 19.0
Eppelsheim (<i>S. diaphorus</i>) ³	15.0 × 20.0
Tchobrouthchi (Molodova) ⁴	15.0 × 17.0
Titoe Veles (Bulg) ⁵	16.7 × 19.0
Iberia (<i>Metarctos batalleri</i> Viret)	
Sabadell ⁶	16.0 × 17.5
Tarrasa ⁷	15.0 × 17.0
Batallones-1 ¹⁰ (n = 2)	16.4 × 19.25
Baode (Loc.31) Shanxi, PRC ⁸	14.9 × 19.4
Fugu, Shaanxi, PRC ⁹	15.5 × 17.0
Lemudong'o (Kenya) (KNM-NK 45780)	13.4 × 16.9

¹ G. E. Pilgrim (1931), p. 16² J. Melentis (1968), p. 312³ M. Schlosser (1887–90), p. 329⁴ M. Pavlov (1914), p. 43⁵ R. Garevski (1974), p. 190⁶ J. Viret (1929), p. 565⁷ J.F. Villalta Comella & M. Crusafont Pairó (1948), p. 86⁸ O. Zdansky (1924), p. 6⁹ X. Wang (1997), p. 193¹⁰ S. Peigné et al. (2005), p. 230**Figure 3.** *Simocyon* sp. (KNM-NK 45780), left M1 crown in occlusal view. Scale bar = 2 cm.

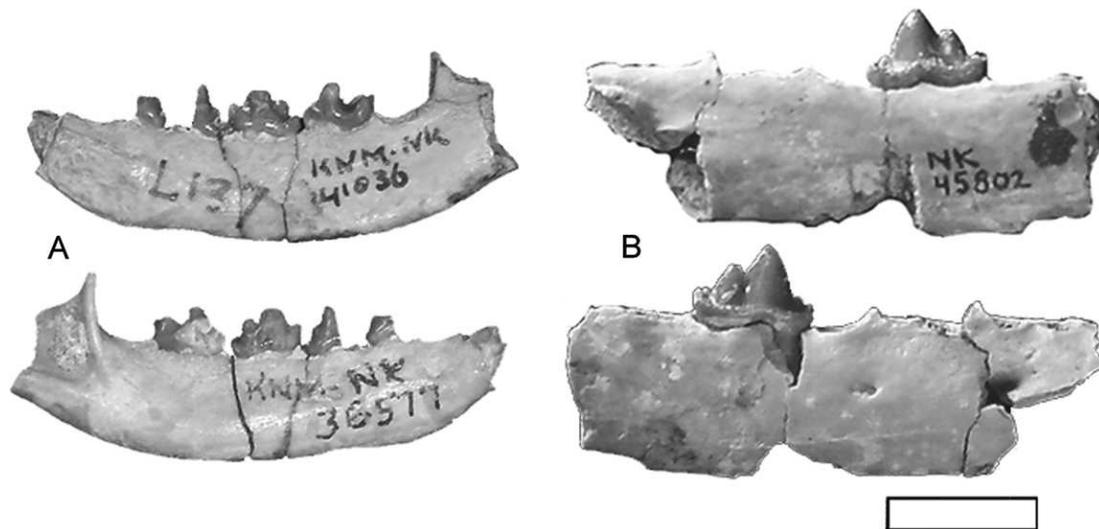


Figure 4. A, *Herpestes* sp. (KNM-NK 36577 and KNM-NK 41036), right mandible in labial (lower) and lingual (upper) view. B, *Ichneumia* aff. *albicauda* (KNM-NK 45802), right mandible with p4 in labial (lower) and lingual (upper) view. Scale bar = 1 cm.

Suborder FELIFORMIA Kretzoi, 1945
 Family HERPESTIDAE Bonaparte, 1845
 Subfamily HERPESTINAE Bonaparte, 1845

Remarks

The late Cenozoic fossil record of African herpestines is overall scant, except for representation at the Laetoli and Olduvai localities. Whether this is due to the lack of screen-washed situations or whether it is a natural circumstance is difficult to establish. At Lemudong'o there are several herpestines now distinguished only by their differences in size. Some are included within the size range of the small mongooses, genus *Helogale*.

Genus *HELOGALE* Gray, 1861
HELOGALE sp.

Description and remarks

KNM-NK 36892 consists of a left horizontal mandibular fragment with partial crown of a p3, and KNM-NK 41114, a right horizontal edentulous mandibular fragment. These two specimens constitute the smallest of the carnivores in the Lemudong'o assemblage. Their fragmentary state and general lack of dentition obviates further identification and attribution. The dwarf mongoose, *Helogale*, is now represented by two species in sub-Saharan Africa, one widely distributed, the other (*H. hirtula*) found only within the northeastern horn of eastern Africa. An apparently extinct, but ill-known species of *Helogale* is known from the upper Miocene of western Afar.

Genus *HERPESTES* Illiger, 1811
HERPESTES species indeterminate
 Figure 4A

Description and remarks

Other remains are within the size range of the genus *Herpestes* and are considered *Herpestes* sp. indet., a form that is somewhat larger than the smallest form attributed above to *Helogale*. There are now four species of *Herpestes* recognized in Africa, two of

which are documented as distributed within Ethiopia. The material consists of: KNM-NK 42319, a right edentulous mandibular fragment with alveolus of m2-m1-p4 and posterior p3; KNM-NK 36577, a right mandibular ramus with partial crown of c, alveolus of p1, broken crowns of p2 and p3 and complete p4; and KNM-NK 41036, a right lower mandibular ramus with talonid and metaconid of m1 and alveoli for m2. These latter mandibular fragments (36577 and 41036) conjoin and thus comprise one nearly complete right mandible body, lacking only the ascending ramus (Figure 4A). They now bear the former number, KNM-NK 36577. This herpestine resembles, and might be the same as, an undescribed, probably new species of *Herpestes* known from the upper Miocene of the western Afar (Ethiopia) (Haile-Selassie, 2001). A small herpestine, referred by Peigné, Salesa, et al. (2005) to the extant *H. (galerells) sanguineus*, and considered by them a distinct genus, is now known from the Toros-Mellala (Chad) locality TM 266, among this older fauna. With the scant material at hand it is difficult to ascertain probable affinities among these finds. Dimensions of some genera and species of herpestines are set out in Table 6.

Genus *ICHNEUMIA* Geoffrey Saint-Hilaire, 1837
ICHNEUMIA aff. *ALBICAUDA* Geoffrey Saint-Hilaire, 1837
 Figure 4B

Description and remarks

KNM-NK 45802, consists of a right p4. This is the largest herpestid of the Lemudong'o association. It matches in size and in morphology the extant white-tailed mongoose, *Ichneumia albicauda*.

Family VIVERRIDAE Gray, 1821
 Subfamily VIVERRINAE Gray, 1821
 Genus *GENETTA* G. Cuvier, 1816
 Figure 5

Remarks

There are remains of two forms of genet, having robust mandibular body and distinguishable by their differences in size (Table 7a).

Table 6. Some lower dentition dimensions (crown length; mm) of Mio-Pliocene herpestines and of extant herpestines.

Taxon	p4	m1	Notes
<i>Ichneumia albicauda</i> KNM-NK 45802	7.5		
<i>Herpestes</i> sp. KNM-NK 36577	4.45		
Herpestidae indet, BAR-1085'99; 2638'03 ⁴	4.5	6.0	4
<i>Herpestes</i> sp. A, Lbwg ¹ L-11847	5.75	6.7, 6.8	1
<i>Herpestes</i> sp. B, Lbwg ² L-16177a	3.75	4.2, 4.3	2
<i>Herpestes</i> sp., Klein Zee ¹ 1930. x1, 5.	5.5, 5.2	6.8, 6.3	1
<i>Herpestes</i> sp., MALM ³ ALA 2/314	4.55	6.3	3
<i>Herpestes</i> sp., MALM ³ ASK 3/64	5.9	—	3
<i>H. (Galerella) sanguinea</i> , TM-266 ⁵	5.0	6.0	5
<i>Herpestes</i> sp., Dhok Pathan, Siwalks ⁶ , GSP-217	7.3	—	6
<i>Atilax paludinosus</i>	8.5	10.0	J. A. Allen 1924
<i>Bdeogale nigripes</i>	7.8	8.5	J. A. Allen 1924
<i>Crossarchus alexandri</i>	6.0	7.1	J. A. Allen 1924
<i>Helogale hirtula</i>	5.7	5.7	J. A. Allen 1924
<i>Helogale hirtula</i> (3)	3.6	4.0 (3.8–4.3)	G. Petter 1987
<i>Herpestes (G.) sanguineus</i>	6.5	8.3	J. A. Allen 1924
<i>Herpestes (G.) sanguineus</i> (21)	4.67 (4.1–5.4)	5.36 (5.0–6.2)	G. Petter 1987
<i>Herpestes (H.) ichneumon</i>	7.6	9.0	J. A. Allen 1924
<i>Herpestes (H.) ichneumon</i> (21)	8.78 (8.1–9.5)	4.7 (4.0–5.0)	G. Petter 1987
<i>Herpestes naso</i>	8.0	9.0	J. A. Allen 1924
<i>Herpestes (G.) pulverulenta</i> (19)	5.45 (5.0–6.0)	6.10 (5.6–6.8)	G. Petter 1987
<i>Mungos mungo</i>	6.9	7.5	J. A. Allen 1924
<i>Mungos mungo</i> (22)	4.89 (4.3–5.3)	(4.2–5.8)	G. Petter 1987
<i>Ichneumia albicauda</i>	7.6	8.1	J. A. Allen 1924

¹ Hendeby (1974) considers Lbwg sp. A as 'virtually indistinguishable' from Klein Zee 1930. x1, 5. (in Stromer, 1931)

² Hendeby (1974) considered sp. B comparable to *Herpestes sanguineus*

³ Haile-Selassie (2001) considers these and other MALM specimens of similar morphology and to constitute same, probably new *Herpestes* species; it is smaller than *H. ichneumon* and *H. (G.) palaeoserengensis*; but is much larger than Lbwg. *Herpestes* sp. B. It is similar in size and some morphology to *H. pulverulenta*

⁴ Herpestidae indet, Tabarin, Baringo (after Morales et al., 2005)

⁵ *H. (Galerella) sanguinea*, Toros-Menalla (Chad) (after S. Peigné et al., 2005)

⁶ Barry (1983) reported on various herpestine dental/gnathic elements from the Pakistan Siwaliks, and considered that several taxa, based on size, were likely represented. The GSP-217 mandible fragment with p4 is of a size and morphology comparable to extant *H. ichneumon*

GENETTA sp. indet. "X"

Figure 5A

Description and remarks

KNM-NK 36581 consists of a fragment of a right mandible body with p4-m1 and root/alveolus of m2. KNM-NK 36578 is a fragment of right mandible body with p3 and the anterior cusp (only) of p4. These two mandible fragments represent parts of different individuals.

Both mandible fragments (36581 and 36578) constitute a large form of genet, and perhaps different from others described heretofore. The body of the mandible is thick and deep and has a very straight inferior border. This contrasts with the curved body figured as *Genetta* sp. A and *Genetta* sp. B at Lothagam (Werdelin, 2003a, p. 279). The masseteric fossa extends to the posterior end of the m2. The p4 has a distinct though small anterior accessory cusp set lingually. In this area a cingulum originates that extends over the labial side of the crown to reach the posterior edge, where it becomes more robust and individuated slightly lingual to the mid-line. The main (protocone) cusp is high and pointed. The posterior accessory cusp is very distinct and is set slightly labially.

The lower carnassial (m1) exhibits high trigonid cusps and a broad talonid. This is unlike the narrow talonid of the Kanapoi specimen (*Genetta* sp. nov.) figured by Werdelin (2003b, p. 130). Paraconid

and protoconid are similar in size and together compose a blade set 45° to the main axis of the crown, as described in the Kanapoi specimen. This orientation of the blade is observed in a number of modern genets. The metaconid is set directly posterior to the paraconid and diverges from the midline toward the lingual side.

The Lemudong'o *Genetta* sp. "X" differs also from the Kanapoi specimen in having a slightly larger alveolus of m2.

GENETTA sp. indet. "Y"

Figure 5B

Description and remarks

Four specimens comprise largely edentulous mandible fragments of a small genet species. These are: KNM-NK 38310, a right mandible fragment with alveoli and p3 crown; KNM-NK 36595, a right mandible fragment with p and m alveoli; KNM-NK 36927, a left anterior mandible fragment with p alveoli; and KNM-NK 42320, a right posterior mandible fragment with m alveoli.

This form ("Y") is overall smaller than specimens referred to *Genetta* sp. "X." The material is clearly insufficient to seek to ascertain specific affinities except by exclusion from known extinct (and extant) larger species. Genet remains of comparable or still younger age are known from some other African localities, among them: Langebaanweg (South Africa), Klein Zee (Nami-

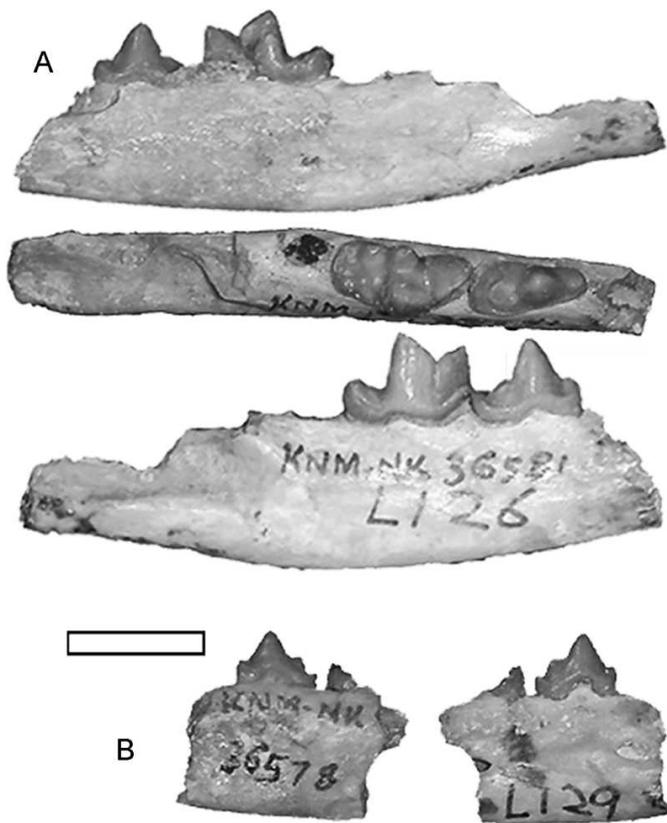


Figure 5. A, *Genetta* sp. indet “X” (KMN-NK 36581), right mandible with p4-m1 in lingual (top), occlusal (middle), and labial (bottom) view. B, *Genetta* sp. indet “Y” (KMN-NK 36578), right mandible with p3 in labial and lingual view. Scale bar = 1 cm.

bia), Lukeino (Kenya), Lothagam (Kenya), Kanapoi (Kenya), some late Miocene localities (MALM) of the Middle Awash, Afar (Ethiopia), and Beni Mellal (Morocco).

Genetta is often considered to comprise some nine species, essentially in sub-Saharan Africa, except for a single species reaching into southwest Europe and Arabia. These are: *G. genetta*, *G. tigrina*, *G. angolensis*, *G. servalina*, *G. victoriae*, *G. abyssinica*, *G. thierryi*, *G. johnstoni*, and *G. maculata* (Wilson and Reeder, 1993). *G. genetta* is a (late) Holocene introduction into countries of Western Europe. Those documented for Ethiopia and the adjacent Horn are *G. genetta*, *G. abyssinica*, and *G. rubiginosa* (that may or may not be a part of *G. tigrina*). The relevant comparative dimensions of six of the lesser taxa, and two other samples comprising their subspecies, are set out in Table 7b.

Following new molecular (cytochrome b) sequence analysis, combined with morphological character (some 50) studies, a total of sixteen species were differentiated (Gaubert et al., 2004). Some have previously been considered as subspecies of the aforementioned taxa. In their newest overview (Gaubert, Taylor, Fernandes, et al., 2005; Gaubert, Taylor, and Veron, 2005), 17 species are recognized in all (number after each indicate number of existent sympoteic species): *G. ayssinia* (2), *G. angolensis* (4), *G. bourloni* (3), *G. cristata*, (2), *G. felina* (4), *G. genetta* (3), *G. johnstoni* (3), *G. letabae* (3), *G. maculata* (9), *G. pardina* (5), *G. piscivora* (4), *G. poensis* (6), *G. schoutendeni* (8), *G. servalina* (5), *G. thierry* (3), *G. tigrina* (2), and *G. victoriae* (4). (Comparative dimensions of cheek teeth of some extant African *Genetta* are given in Table 7B). This is

Table 7A. Comparative mandibular cheek-tooth dimensions (mm) in African *Genetta* spp. of late Miocene Age.

	Lothagam ¹		Kanapoi ²		Klein Zee ³		MALM ⁴		Lemudong'o		Kapsomin (Lukeino Fm) ⁵	
	<i>Genetta</i> sp. A	<i>Genetta</i> sp. B	<i>Genetta</i> sp. nov.	<i>Genetta</i> sp.	<i>Genetta</i> sp.	<i>Genetta</i> spp.	<i>Genetta</i> spp.	<i>Genetta</i> sp. 'X'	<i>Genetta</i> sp. indet.			
	KNM-LT 25409	KNM-LT 23945	KNM-KP32815	1930. XI-6a	ADD-1/7	AME-1/43	ALA 2/169	KNM-NK 36581	KNM-NK 36578	BAR 155701		
Lp3	5.3			5.0					5.8			
Wp3	2.8			2.5					2.3			
Lp4	5.9	(5.1)		5.6				8.1				
Wp4	3.1	2.6		3				3.6				
Lpp4	3	2.3						4.3				
Lm1				6.5	7.0	8.9	6.96	9.3			8.5	
Ltm1	5.3							6.8				
Wm1	3.9			3.2	3.6	3.6	—	5.2			4.0	
Hm1	8.9			8.0				11				

¹ Werdélin (2003a)

² Werdélin (2003b)

³ Stromer (1931)

⁴ Hailé-Selassie (2001)

⁵ Morales et al. (2005)

Table 7B. Comparative cheek tooth dimensions (mm) in some extant African species of *Genetta*. The L (length), W (width), and H (Height) diameters are self evident. Lpp (length of protocone cusp of p) and Ltm1 (length of lower molar trigonid) are evidently less so.

	<i>G. genetta</i> n = 4	<i>G. tigrina</i> n = 6	<i>G. angolensis</i> n = 5	<i>G. servalina</i> n = 7	<i>G. victoriae</i> n = 6	<i>G. maculata</i> n = 6	<i>G. schoutedeni</i> n = 6	<i>G. johnstoni</i> n = 2
QBH 1974	QBH 1974	RJ 2005	RJ 2005	RJ 2005	RJ 2005	RJ 2005	RJ 2005	RJ 2005
Lp3	6.4 (6.2–6.5)	6.0 (5.6–6.2)						
Wp3	2.3 (2.2–2.3)	2.4 (2.2–2.5)						
Lp4	6.6 (6.5–6.7)	6.7 (6.1–6.9)	6.13 (5.73–6.58)	6.12 (5.78–6.65)	7.94 (7.43–8.38)	6.14 (5.65–6.87)	8.26 (5.26–6.73)	5.3
Wp4	2.8 (2.7–2.8)	2.9 (2.7–3.1)	2.72 (2.53–3.1)	2.41 (2.17–2.54)	3.69 (3.39–4.1)	2.68 (2.31–3.09)	2.72 (2.35–3.11)	1.8
Lpp4								
Lm1	7.6 (7.4–7.7)	7.5 (7.2–7.6)	7.4 (7.05–7.93)	6.5 (6.12–7.13)	8.96 (8.11–9.48)	6.91 (6.39–7.1)	7.03 (6.28–7.83)	5.5–6.1
Ltm1								
Wm1	3.8 (3.7–3.9)	3.8 (3.5–4.1)	3.74 (3.44–3.97)	3.38 (2.93–3.75)	4.87 (4.14–5.54)	3.72 (3.26–4.15)	3.82 (3.51–4.08)	2.6–2.7

Measurements from Hendey (1974) and from collections of Musée Royale de l'Afrique Centrale, Tervuren, Belgium, kindly provided by Ms. Rebecca Jabbour (2005)

an important and sweeping revision based on over a dozen museum collections and a sample of over 5,000 specimens. Five such species found within the southern African sub-region—*G. angolensis*, *G. tigrina*, *G. maculata*, *G. genetta*, and *G. felina*—the third and fourth having broadly African distributions, have been examined in depth, their species validity confirmed, and the presence and degree of ocyptic hybridization sometimes confirmed (Gaubert et al., 2005). Molecular assessments (cytochrome b), assuming clocklike behavior, affords estimates of minimum divergence date(s) (mdd) initially within the late Miocene, subsequently within the Pliocene, and ultimately Plio-Pleistocene, even to mid-Pleistocene (Gaubert et al., 2004). Such cladistic hypotheses can and will be testable from the expanding fossil record. At this stage, and given the nature and limitations of the genet samples, it is probably premature to seek to resolve questions of phylogenetic affinities and, hence, their primary systematics.

However, it has been possible to distinguish the principal size morphs (Table 7C).

As often said elsewhere by various investigators, the genus *Genetta* merits further investigation and systematic revision, now particularly that the fossil record is enhanced, although admit-

tedly largely fragmentary. Most importantly it is essential to provide a phylogenetic perspective to the seemingly speciose genus *Genetta* as now known.

Family HYAENIDAE Gray, 1821 (1869)

HYAENICTIS A. Gaudry, 1861

HYAENICTIS aff. *HENDEYI*

Figure 6

Description and remarks

KNM-NK 36598 is a partial right mandible body with p4 and partial roots of p3 and m1 (Table 8). The complete fourth lower right premolar (p4) is almost fully erupted in a partial ramus fragment. It presents a small but distinct anterior accessory cusp and a large trenchant posterior cusp and a high main cusp (pr^d). A posterior cingulum forms a crest that runs from the groove of the principal cusp and posterior accessory cusp (through the lingual face) towards the posterior end of the crown.

The morphology of p4 with its posterior cingulum crest is especially characteristic of the genus *Hyaenictis* and of the lineage (*Hyaenictitherium-Hyaenictis*) (Werdelin et al., 1994). It also fits

Table 7C. Principal size morphs of African species of *Genetta*.

Northern Africa:	Beni Mellal (Morocco) A diverse vertebrate assemblage, of attributed pre-Vallesian affinity (and age), including amphicyonid, mustelids (2), hyaenids (2), a small feline and a viverrine (Ginsburg, 1977). The latter is clearly a <i>Genetta</i> sp., about the size of <i>G. tigrina</i> . It comprises only an M2 and mandible with dp4 (5.2 × 2.25), not sufficient for a systematic attribution.
Eastern Africa:	Lothagam (Kenya) <i>Genetta</i> sp. A (LT-25409), from the lower Nawata formation, about the size of <i>G. servalina</i> (Werdelin, 2003a). It may also be represented at MALM/Ethiopia by ALA-2/199 (Haile-Selassie, 2001). <i>G. sp. B.</i> (LT-23945), from the upper Nawata formation, is a smaller form (by about 20%), and perhaps about the (dental) size of <i>G. johnstoni</i> . Kapsomin , Lukeino Formation (Kenya) A single left m1 (BAR 155 '01) that is referred to, and clearly represents <i>Genetta</i> sp. (Morales et al., 2005). Its species affiliation remains unresolved, although it is close morphologically to <i>G. genetta</i> though rather larger and having an enlarged talonid. In size it is not distant from a MALM (Ethiopia) specimen, AME-1/43. Kanapoi (Kenya) <i>G. sp. C</i> (KP-32565, 32815) a larger form about comparable (dentally) in size to <i>G. genetta</i> . MALM (Ethiopia) ADD-1/17, a form with morphological distinctiveness suggestive of a <i>Genetta</i> sp. nov. D. Lemudong'o (Kenya) A larger form, <i>G. sp. "X,"</i> dentally comparable in size to extant <i>G. victoriae</i> , and seemingly distinct morphologically from <i>G. sp. A</i> and <i>B</i> (Lothagam) and from <i>G. sp. C.</i> (Kanapoi).
Southern Africa:	Klein Zee (Namibia) A larger form (1930.XI, 6a specimen) comparable in size to <i>G. genetta</i> . Langebaanweg (South Africa) A rather smaller form (L-11191 specimen) comparable in size to <i>G. tigrina</i> .

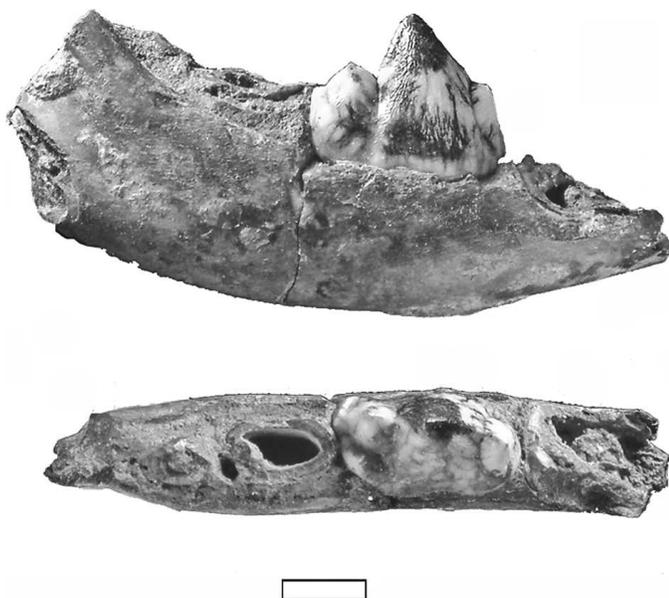


Figure 6. *Hyaenictis* aff. *hendeyi* (KNM-NK 36598), right mandible with p4 in labial and occlusal view. Scale bar = 1 cm.

well with the description of *Hyaenictitherium* cf. *H. parvum* from Lothagam (Werdelin 2003a). However, the Lemudong’o specimen is larger than the latter, and is of a size comparable to *Hyaenictis hendeyi*. We suggest attribution to this genus, and possible affinities to *H. hendeyi*.

The genus type, *Hyaenictis graeca* Gaudry, remains still unknown, both in terms of specimens and morphologically (Gaudry, 1861; Werdelin and Solounias, 1991). The genus was first documented in Africa at Langebaanweg (Hendey, 1978a). Important distinctions and relationships between several hyaenid taxa were made by Werdelin et al. (1994), wherein *Hyaenictis hendeyi* sp. nov. was proposed. Cf. *Hyaenictis* sp. has been recognized by Werdelin (2003) at Lothagam (lower Nawata formation), Kenya. In the Tugen Hills, Baringo district (Kenya) remains referred to *H. hendeyi* have been recovered in other Mio-Pliocene formations, notably several localities of Lukeino Formation (6.1–5.7 Ma) and the succedent Mabaget formation (at Tabarin) (5.1–4.5 Ma) (Morales et al., 2005). The remains are exclusively isolated upper or lower teeth, and species identification is insecure. Other attributed remains of *Hyaenictis* sp., probably *H.* sp. nov., derive from localities (AME, AMW and STD) of the MALM/Ethiopia, and are of comparable antiquity (Haile-Selassie,

2001; Haile-Selassie et al., 2004b). It is probable that a form of *Hyaenictis*, termed *H. almerai* Villalta and Crusafont (1943), is represented as well in the Catalan locality of San Miguel de Taudell (Spain), of upper Vallesian (MN-10) age.

Family FELIDAE Gray, 1821
 Subfamily MACHAIRODONTINAE Gill, 1872
 Genus *LOKOTUNJAILURUS* Werdelin, 2003a
LOKOTUNJAILURUS EMAGERITUS Werdelin, 2003
 Figures 7–8

Description and remarks

KNM-NK 36928 comprises most of the crown, minus the distal tip, of a left upper canine. The only material that can be reasonably certainly referred to this sabre-tooth cat is this partial and distal upper canine of large size. The tooth is markedly mediolaterally compressed and both anterior and posterior edges exhibit very fine serrations throughout their length (Figure 7). Thus, this fossil is excluded from consideration as any species of either *Megantereon*, *Dinofelis*, or *Metailurus*. The generic attribution proposed here is based on its very close approximation in overall size and in shape to the upper canine (KNM-LT 25405) of the newly named machairodont from Lothagam (Kenya), *Lokotunjailurus emageritus*, described recently by Werdelin (2003a), and with which it is comparable overall.

KNM-NK 45896 consists of a right proximal femur, from the upper shaft and including neck and head, of a felid similar in size and morphology to *L. emageritus*. The femur was damaged by carnivore ravaging, which largely destroyed the greater trochanter, much of lesser trochanter, and the margins of the articular head (Figure 8). The projected original proximal breadth (66/67 cf. 63/73) and head (32.5 cf. 34.6) diameters are quite suitable to an *L. emageritus* individual.

A damaged proximal portion of left mt-3 (KNM-NK 45789) represents a felid of at least medium size (Figure 8). It is questionably included here with *L. emageritus*, but without a formal attribution.

A substantial larger element (KNM-NK 44755), perhaps mc-3/4, comprising a good part of the diaphysis, up to but not including the proximal articulation, is also felid, but of still unknown affinity.

This is only the second record of the machairodont *Lokotunjailurus emageritus* Werdelin, first recorded from the Nawata Formation, Lothagam, both lower and upper levels, and including a partial skeleton and other skeletal parts of several individuals. There are reasons put forward in respect to specific aspects of dental (and other) morphology to consider this form as recognizably derived relative to the more commonly known and late *Machairodus*, *M. giganteus*. The latter genus, at least, is

Table 8. Comparative dimensions (mm) of p4 of *Hyaenictis* and of *Hyaenictitherium* spp.

	Lothagam ¹ (Kenya)		Lemudong’o (Kenya)	Langebaanweg ² (S.Africa)		MALM deposits ³ (Ethiopia)	
	<i>Hyaenictitherium</i> cf. <i>H. parvum</i> KNM-LT 10032	<i>Hyaenictis</i> sp. KNM-LT 25057	KNM-LT 23033	<i>Hyaenictis</i> aff. <i>hendeyi</i> KNM-NK 36598	<i>Hyaenictitherium namaquensis</i> (n = 5)	<i>Hyaenictis hendeyi</i> (n = 4)	<i>Hyaenictis</i> sp. nov.
Lp4	18.9	20.7	20.9	23.1	20.7–21.52	22.8–26.0	19.5–19.8; 21.2
Wp4	9.4	9.8	10.9	12.5	10.8–11.3	11.7–13.2	10.9–11.1; 11.3
Lpp4	9.9		9.5	10.7	10.2–10.9	10.6–12.0	

¹ Werdelin (2003a)

² Werdelin et al. (1994)

³ Haile-Selassie (2001)



Figure 7. *Lokotunjailurus emageritus* (KNM-NK 36928). left upper canine in labial and lingual view. Scale bar 2 = cm.

elsewhere represented (in Africa) at Wadi Natrun (Egypt), at Sahabi (Libya), and at Langebaanweg (South Africa).

Subfamily FELINAE Trouessart, 1885
Genus *LEPTAILURUS* Severtzon, 1858

Description and remarks

KNM-NK 42269 consists of a fragment of a right m1. This fragmentary first lower molar represents a small-sized felid. It is incomplete, and hence affords no measurements. Its small size and observable morphology is comparable to that of *Leptailurus*, the serval.

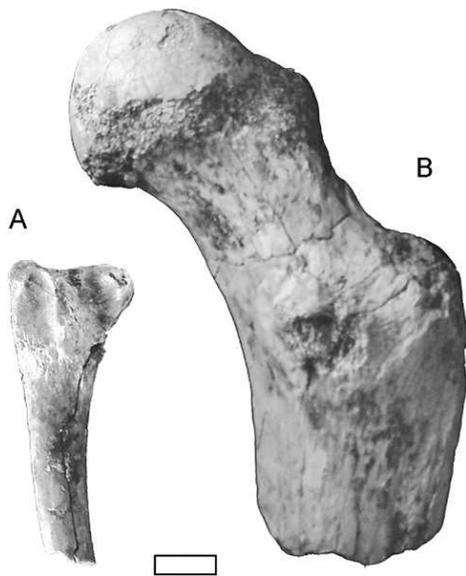


Figure 8. *Lokotunjailurus emageritus*: (KNM-NK 45789) left metatarsal (A) and (KNM-NK 45896) right proximal femur (B). Scale bar = 2 cm.



Figure 9. *Metailurus major* (KNM-NK 45832), left mandible with p3 and p4. Scale bar = 1 cm.

Subfamily FELINAE Trouessart, 1885
METAILURUS Zdansky, 1924
METAILURUS MAJOR Zdansky, 1924
Figure 9

Description and remarks

KNM-NK 45832 consists of a portion of the alveolar part of a left mandible body with well preserved p3 and p4. The size and morphology of the dentition replicates that of the widely distributed, but still incompletely (postcranially) known feline, *Metailurus major* Zdansky. The p3 has a low, broad cusplet below a salient anterior crest; the pac (posterior accessory cusp) is a distinct cusplet, at the base of a posterior crest with which it is aligned; another small accessory cusplet is set disto-lingually near that margin of the talonid. The p4 is a much larger tooth, with notably enlarged and salient aac (anterior accessory cusp) mesial to a salient anterior crest; the talonid is markedly broadened, particularly medially, with an uplifted shelflike, encircling, thickened cingulum; the pac (posterior accessory cusp), somewhat worn, is substantial and was apparently once rather larger than its mesial counterpart. Another exterior p3 fragment (KNM-NK 45863), bearing a small pac, is most parsimoniously also referred to *M. major* on the basis of comparable size and morphology. Dimensions of this and other specimens of the *M. major* are set out in Table 9.

This genus, and its initially recognized species, was first (Zdansky, 1924) and perhaps is still best known in eastern Asia (China), from which it has been reported at multiple upper Miocene fossiliferous localities (eg., Yushe, Baote). It has been found in central Europe (Polgardi, Hungary), in mainland (Pikermi, Halmypotamus) and insular (Samos) Greece, in the western Appennine peninsula (Baccinello V3, Italy), and at localities in the Iberian Peninsula of Spain (Alfacar, Ademuz, and Concud). It is essentially a component of latest Miocene age (Turolian) faunal assemblages (Ginsburg, 1999). It has been certainly documented previously in Africa only at the Lothagam locality (Kenya), from its Nawata Formation, and largely by a few postcrania and a distinctive upper canine (Werdelin, 2003a). And, the Lukeino Formation (Kapsomin) has yielded a partial maxilla with P3 referred recently by Morales et al. (2005) to

Table 9. Some dental dimensions (mm) of *Metailurus major* specimens. Sources of metrics: 1 = Zdansky (1924, p. 125, 127); 2 = Chang and Houyi (1964, p. 183, 184); 3 = Teilhard de Chardin and LeRoy (1945, p. 21); 4 = Roussiakis (2001, p. 124); 5 = Melentis (1968), metrics in S. Roussiakis (2001, p. 124); 6 = Rook, Ficarelli, and Torre (1991, p. 12); 7 = Morales and Soria (1979, p. 498); 8 = Pons-Moya (1987, p. 67) (this distinctive Metailurine was designated as the type of *Fortunicteis acerensis*).

	Paôte ¹ Loc. 30 (Shansi) Type	Xialou ² (Shansi)	Yushé ³ (Shansi)	Pikermi ⁴ (Gr)	Halmypopotamus ⁵ (Gr)	Baccinello V3 ⁶ (It.)	Concud, Teruel ⁷ (Sp.)	Casa de Acero, Teruel ⁸ (Sp.)	Lemudong'o (Kenya)
		v. 2896/1+2	un-numbered	P.A. 1257/91 P.G. 95/1532	1967/1				KNM-NK 45832
P3	20.2 × 8.9	16.3 × 8.5	20.0 × 10.0	19.0 × 9.7 18.8 × 9.6	19.0 × (10.2) 18.8 × (9.7)			19.7 × 9.0	
P4	31.2 × 14.0	29.0 × 12.5	32.0 × 16.0	29.7 × 14.1 28.9 × 14.9	(28.8) × (13.8) — × 14.5			30.8 × 14.3	
M1	5.5 × 11.9	5.0 × 8.5		5.5 × 12.0 5.9 × 12.5 (4.9) × (12.2)					
			no. 10.368						
p3	15.5 × 8.4	12.5 × 6.0	14.0 × 8.0				15.0 × —		13.0 × 7.6
p4	21.0 × 9.3	18.5 × 8.0	21.0 × 9.0			19.9 × 7.8		20.2 × 8.4	18.6 × 9.3/8.7
m1	23.2 × 10.1	21.5 × 10. —	24.0 × 10			21.1 × 8.6	23.5 × 10.0	23.8 × 9.5	

this genus, and apparently a smaller species. A related metailurin—*Fortunicteis*—is recorded at Casa del Acero (Fortuna basin), Spain (Pons Moya, 1987).

Discussion

Lemudong'o is but one of an increasing number of African fossiliferous localities of late Miocene age. Those that have yielded representatives of the order Carnivora are set out in Table 10. This effort affords some insight, as reliable information permits, on taxonomic representation and diversity. The columns are expressed strictly geographically, reading from north to south by scanning from left to right. Some such localities are not listed although having afforded one or more taxa of particular interest or significance; attention may be drawn to several such in the following comments.

The maximum span of concern, the upper Miocene, is arbitrarily delimited as between just over eleven million (11.1) and just under five (4.9) million years ago (Ma) (Steininger, 1999). In western Eurasia, including the peri-Mediterranean region, this encompasses the two last European Land Mammal Megazones (ELMMZ) of the Miocene, the Turolian and antecedent Vallesian zones. Their respective subdivisions are tripartite (MN-11, 12, and 13) and bipartite (MN-9, 10) and, in aggregate, are now estimated to encompass the time between 8.7 and 4.9 Ma, and between 11.1 and 8.7 Ma, respectively. All of the fossiliferous localities enumerated in Table 10 are either of known radiometric (isotopic)-determined age or of biostratigraphically-based estimated age as correlative with the younger, Turolian, ELMMZ. There are a few African localities of Vallesian-equivalent age, in both northwest (the Maghreb) Africa and in eastern Africa; however, still fewer yield remains of Carnivora (see below), and even then some remain unstudied (or insufficiently reported). Some localities, in particular those of Lothagam and of Sahabi, are known to, or must have sampled, a considerable range of time. At Lothagam the bulk of the vertebrates derived from the lower (7.4–6.5 Ma) of two members of the Nawata Formation, with at least nine taxa persisting into the overlying upper member (6.5–5.0 Ma, extrapolated age); a few taxa (two or so) recur in the succeedent (lower) Apak Member (of the Nachukui Formation) of lowermost Pliocene age. At Sahabi an uppermost Turolian (MN-13 Zone) age has been considered most probable for much of the (carnivore) assemblage; but, some evidence has been claimed by some workers to indicate

both younger (MN-14) (Bernor and Pavlakis, 1987) and, perhaps, still older (MN-12) ages encompassed within the depositional succession of the Sahabi Formation (Géraads, 1989). These obscurities can, and doubtless will be, clarified through renewed geological and paleomagnetic investigations.

At this stage it is probably the wiser course to consider the available documentation rather subjectively. It would be misleading to employ one or more measures (indexes) of faunal diversity, as commonly applied, in view of the preliminary and incomplete state of alpha taxonomy and, particularly, the absence of requisite comparative analyses of lineage components purportedly represented at multiple localities. Hence, it is best to err on the more conservative side.

The entries of Table 10 reveal that an increasingly better, that is more inclusive, representation of the order Carnivora is now emerging for roughly the last three million years of the African Miocene. It should be noted that such fossil localities span the length of the African continent, and there are a number in the Mediterranean area, one in the southernmost subcontinent, and an increasing number in sub-equatorial reaches of eastern Africa. Others, still under investigation and awaiting study and publication, sample sub-Mediterranean reaches of northern Chad.

Eleven mammalian families are represented: five Feliformia (Felidae, Viverridae, Herpestidae, Hyaenidae, Nandiniidae); one Cynoidea (Canidae); three Arctoidea (Ursidae, Amphicyonidae, Phocidae); and two Mustelida (Mustelidae, Procyonidae). The number of genera approaches 40. The recognizable species of large- to mid-sized taxa are in number, at least, as follows: Felidae (5); Hyaenidae (7); Canidae (2); Ursidae (2); Amphicyonidae (3); Phocidae (2); Mustelidae (10); and Procyonidae (1). The number of lesser-size species might well equal half of this number, if the available fossil evidence ultimately proves satisfactorily amenable to taxonomic resolution, in respect to small felines, and to viverrids and herpestids.

Among the Felinae the genera *Metailurus* and *Dinofelis* have Eurasian affinities, if not actual roots, and are characteristic of this interval in Africa. The lesser cats are less well-represented and certainly very imperfectly known overall. One or more caracal/lynxlike forms and a serval are demonstrably represented, again with both extra-African and, perhaps, autochthonous affinities.

Several machairodontine felids occur in this and the antecedent time span in Africa. *Machairodus* has been commonly recognized,

Table 10. Current status of distribution of Carnivora in African upper Miocene local faunas (sources within text).

Taxon	Sahabi (Libya)	Wadi Natrun (Egypt)	MALM (Ethiopia)	Lothagam (Kenya)	Lukeino (Kenya)	Mabaget (Kenya)	Lemudong'o (Kenya)	Langebaanweg (So. Africa)	Klein Zee (Namibia)	Kanapoi (Kenya)
FELIFORMIA										
Felidae										
Felinae										
<i>Metailurus major</i>				cf.	sp.		+			
<i>Dinofelis diastemata</i>			+	sp.	+			+		
<i>D. petteri</i>										+
<i>F. (Leptailurus) serval</i>							cf.	+		
<i>F. (Lynx) issiodorensis</i>								+		
<i>Felis</i> sp.										+
Felinae indet.	+					+		+		
Machairodontinae										
<i>Machairodus</i> sp.	+	cf.	sp.					+		
<i>Lokotunjailurus emargeritus</i>				+			sp.			
<i>Homotherium</i> sp.								+		+
? <i>Megantereon obscura</i>								+		
Viverridae										
<i>Viverra (Megaviverra) leakeyi</i>	+		+	+	+			+		
<i>Viverra howelli</i>	+			cf.						
Viverrinae indet.	+									
<i>Genetta</i> sp.			+	sp. A, sp. B	sp.		sp. X, sp. Y	+	+	sp. nov
<i>Civettictis howelli</i>						+				
Herpestidae										
<i>Helogale</i> sp.			+				sp.			+
<i>Herpestes</i> sp.			sp. nov.		indet.		spp. indet.	spp. A,B,C,D,E	sp.	
<i>Ichneumia albicauda</i>					cf. sp.		+			
Nandinidae										
<i>Nandinia</i> sp.					+					
Hyaenidae										
<i>Ikelohyaena abronia</i>				cf.		+		+		
<i>Hyaenictis hendeyi</i>	cf.		sp.nov	cf. <i>H.</i> sp.	sp.	+	sp.	+		
<i>Chasmaporthetes australis</i>	sp.							+		
<i>Hyaenictitherium namaquensis</i>	sp.	+	+	cf. <i>H. parvum</i>		+		+	+	
<i>Adcrocuta eximia</i>	+									
<i>Ictitherium</i> sp.				ebu						
<i>A. (Dinocrocuta) senyureki</i>	cf.									
<i>Parahyaena howelli</i>										+
CYNOIDEA										
Canidae										
<i>Vulpes</i> sp.								+		
<i>Eucyon intrepidus</i>						+	aff.			
ARCTOIDEA										
URSIDA										
Ursidae										
<i>Indarctos</i> sp.	+									
<i>Agriotherium africanum</i>	sp.		sp.					+		
<i>Agriotherium aecuatorialis</i>						+				
Amphicyonidae										
Phocidae										
<i>Homiphoca capensis</i>								+		
<i>Monachina</i> indet.	+									
<i>Pliophoca etrusca</i>		+								
MUSTELIDA										
Mustelidae										
Lutrinae										
<i>Vishnuonyx angolensis</i>				+						
<i>Sivaonyx africana</i>					+					
<i>Enhydriodon hendeyi</i>			+			sp.		+	+	ekecaman sp.
<i>Torolutra ougandensis</i>						+				
Lutrinae gen./sp. indet.		+	+							
Mellivorinae										
<i>Mellivora benfieldi</i>			+					+		
<i>Ekorus ekakeran</i>				+						
<i>Erokomellivora lothagamensis</i>				+						
Mellivorinae indet.				+						
Guloninae										
<i>Plesiogulo botori</i>			+				+			
<i>Plesiogulo monspessulanus</i>								+		
<i>Plesiogulo praecocidens</i>						+				
Procyonidae										
Simocyoninae										
<i>Simocyon</i> sp.							+			

sometimes without certain specific designation, but apparently comparable to *M. giganteus* in size. *M. robinsoni* was proposed on the basis of incomplete mandible body and upper canine from (upper) Beglia Formation, Tunisia; it is *M. aphanistus*-like, but rather smaller (Kurtén, 1976).

An uncommonly large form, attributed to *M. kabir* sp. nov. (Peigné, de Bonis, et al., 2005), has recently been recognized from a locality (TM-266) in the Toros-Menalla area (northern Chad) in a (lower) Turolian-equivalent faunal context. The recognition of *Lokotunjailurus* (at Lothagam), through the Nawata Formation, raises the possibility that this taxon may be represented elsewhere (perhaps among the MALM localities), as suggested here also for Lemudong'o. Moreover the roots of this form remain unknown and, for the moment, unresolved. A once enigmatic "machairodontine," termed *Vampyriictis vipera* (Kurtén, 1976), occurs in the (lower), pre-Vallesian age Beglia Formation (Tunisia); it is distinct in upper canine and lower carnassial morphology and now considered a member of Barbour's felinae (see McKenna and Bell, 1997), along with *Sansanosmilus* (Eurasia) and *Syrtosmilus* (Africa).

This void is in spite of the often acknowledged presence of upwards of a purported dozen species, in western Eurasia alone, of *Machairodus*—*M. pseudailuroides*, *M. romeri* (both Turkey), *M. kurteni*, *M. laskaveri*, *M. aphanistus*, *M. giganteus*, *M. copei*, *M. alberdiae*, *M. irtyschensis*, and *M. taracliensis*. There is a single instance, probably valid, of the presence of *Homotherium*, whose roots are otherwise ill-appreciated.

Those lesser carnivores, viverrids and herpestids, are actually not so rare, given appropriate recovery procedures in the proper sedimentary paleoenvironments. However, as there are only generally fragmentary gnathic/dental remains, and modern systematic and phylogenetic evaluation is still needed, there remains substantial uncertainty at the specific level. None the less, the former family is not infrequently represented, notably by the large viverrine *V. (Megaviverra) leakeyi*, rarely by another smaller taxon, recently named *V. howelli* Rook and Martinez-Navarro, 2004, and the almost ubiquitous African genus *Genetta*. There may be more than six species in the now known African late Cenozoic record. Three antecedent genera—the common, poly-specific *Semigenetta*, and *Viverrictis* and *Plioviverrops*—are not uncommon in the west Eurasian Miocene.

Herpestids, better represented in the Plio-Pleistocene, are now coming to be better known in the African Mio-Pliocene. Certainly there are manifold mongoose species of *Herpestes* represented in the known record, differentiated both in terms of size and, to an extent, morphology; however, this family certainly requires revision. Fuller knowledge of each of these families is in fact requisite toward more comprehensive insight of biogeographic relations with southern Asia.

Hyaenidae are now probably the best represented and hence best known of upper Miocene African Carnivora. However, the documentation of taxa is still very uneven, and the overall skeletal biology per taxon is most unevenly, if at all known. Led by the familial revision by Werdelin and Solounias (1991), building on earlier work by Howell and Petter (1980, 1985), the former constitutes a most impressive, comprehensive, and effective undertaking; it has enabled major progress in the clarification of the systematics, synonymy, and phylogenetics of this important pan-continental mammalian group.

The African group comprises endemic taxa (*Ikelohyaena*, *Parahyaena*), those of Afro-Asian affinity (*Chasmaporthetes*, *Hyaenictitherium*), those of Afro-Palaearctic affinity (*Adcrocuta*, *Ictitherinae*, and *Percrocuta*), and those of Afro-European

affinity (*Hyaenictis*). Such differentiation is probably both oversimplified and, to an extent, inadequate. It is, however, suggestive. Although the presence of some distinctive clades has begun to emerge, as Werdelin and Solounias (1991) and some others have discerned, there remains much in the way of uncertainty, not to mention mystery in regards to affinities, origins, distributions, and extinctions among them. Other ranges (Vallesian-equivalent) of the African upper-Miocene yield different, and mostly quite unrelated "hyaenoid" taxa. These include percrocotids (Percrocotidae) and, if as accepted by some, allohyaenids (genus *Allohyaena*), and the gigantic *Dinocrocuta*. We confess that the higher taxonomy in this matter is clearly muddled and in need of study and revision. The African occurrence of *Percrocuta tobieni* (Ngorora; Bled Douarah) parallels that (earlier) of *P. miocenica* (Croatia), and of *P. abassalomi* (Georgia), in MN-6. A very large (allohyaenid) is *A. (Dinocrocuta) algeriensis* (Bou Hanifia, Menacer, Algeria) and, perhaps, *A. (ex-Hyperhyaena) (D.) leakeyi* (Nakali, Kenya). The type is *Allohyaena kadici* (Csákvár, Hungary). The genus is also known in Ukraine, where it is represented by *A. sarmatica*. And, other taxa are *A. (D.) salonicae* (Thessaloniki, Greece, probably MN-9), *A. (D.) senyureki* (Yassioren, Turkey, MN-9) and several other localities, as at Sahabi (Libya). The Asian counterpart is (*Dinocrocuta*) *gigantea* (Gansu). It is worth noting that the Beni Mellal (Morocco) locality purportedly yields a form (*graeca*) of *Hyaenictis*, said to be the same as the holotype species from Pikermi (this, however, might equally well be a *Hyaenictitherium*) as well as an icitther (I. cf. *arambourgi* Ozansoy), purportedly like the type species from the Sinap, Anatolia. Two hyaenids occur in another pre-Vallesian age mammal assemblage at Bled Douarah (Beglia formation), an icitther (*Protictitherium punicum*) and an indeterminate *Lycyaena* species. In the still older, and mid-Miocene age locality of Arrisdrift (Namibia) no hyaenids are represented at all, although six other carnivore families (nine species) are quite adequately documented (Morales et al., 1998).

The palm civet (*Nandinia binotata*), now considered part of a separate family (and that is otherwise Asian in distribution), is almost unknown in the African fossil record. There is now a single occurrence of the genus reported from Lukeino. It is largely tied to pan-African, peri-equatorial tropical forests, and including those eastern montane areas extending meridionally from Kenya toward Zimbabwe.

The presence within Cynoidea of the subfamily Caninae (within Canidae) within the upper Cenozoic of (western) North America came to light almost a century ago. It was repeatedly confirmed, particularly in Hemphillian local faunas, without any counterpart in the western Palearctic until some 50 years ago. *Canis cipio* is still the oldest occurrence in western Eurasia (in MN-12, mid-Turolian) at Concud, and maybe, at Los Mansuetos (Spain). (Both *Vulpes* and *Nyctereutes* have long been known to occur later, in MN-15 (mid-Pliocene) in Mediterranean Europe.) In recent decades the presence of North American *Eucyon* in eastern Asia has been securely documented. And, there are now multiple occurrences—at South Turkwell, at Lukeino, and at Lemudong'o, and probably elsewhere as well—in equatorial Africa of this same taxon, but of slightly younger age, somewhat over 6 Ma. Unfortunately, the documentation remains fragmentary, but the general pattern of the dispersal westwards through the Palearctic into the Ethiopian realm is at least established. The definition of species of *Eucyon* in Asia, as well as of *Nyctereutes* and, to an extent *Vulpes* within Eurasia, has similarly been enabled by significant fossil documentation across these continents.

Ursids have long been Palearctic in distribution. The Miocene witnessed the ultimate demise of older subfamilies and the appearance of ursines. Two major taxa, *Indarctos* and *Agriotherium*, of older origins are significant members of Holarctic faunas of later Tertiary age. The former is more speciose than the latter in the Palearctic, and constitute trans-Beringian Asian emigrants into the Americas. The trans-continental dispersal of both taxa, some 8–7 million years ago, along with other important elements (*Machairodus*, and Mustelida-like *Simocyon*, *Plesiogulo*, and *Eomellivora*) is now well documented (Qiu, 2003). They are representative of Vallesian and/or Turolian age local faunas. *Indarctos* has only been documented in Mediterranean Africa, at the Sahabi and Menacer (Algeria) localities. *Agriotherium africanum* occurs in quantity, and in excellent preservation at Langebannweg. The genus is recorded at Sahabi and in the western rift (Uganda), and a new species, *A. accuratorialis*, recently was documented at Mapaget (Tugen Hills, Baringo basin, Kenya) (Morales et al., 2005).

The arctoid family Amphicyonidae (bear dogs) was among the most successful, persistent, and speciose family among the larger Cenozoic carnivores. The roots of amphicyonoids are in the Paleogene. Diverse genera dispersed from (east) Eurasia through Beringia into North America in the course of the earlier Miocene. One of, if not, the last African occurrences known is that at Lothagam in which larger (A) and smaller (B) species have been found to persist there in successive levels of the Nawata formation (Werdelin, 2003a). Their phylogenetic affiliations are still unknown, although the smaller might constitute a unique and new genus. This is later than the youngest known (upper) Miocene occurrence (that is, MN-9) in Europe and, perhaps, even within Eurasia. Other occurrences of slightly older, but still upper Miocene age, are known at Beni Mellal, Morocco (*Agnotherium* cf. *antiquum*) and similarly as well as also rather older at Bled Douarah (Begli Formation, Tunisia), at Qued Mya-I, Tademaït, Algeria (and, termed *Myacyon dojambir* Sudre and Hertenberger [1992, p. 107–109]), and at Kabasero, Ngorora (Kenya, also an *Agnotherium*). Middle Miocene occurrences are at Fort Ternan, Kenya (*Agnotherium* sp.), at Djebel Zelten, Libya (*Afrocyon burolleti* Arambourg n. g., n. sp.), and at Arrisdraft, Orange River, Namibia (*Amphicyon giganteus* and *Ysengrinia ginsburgi*) (Morales, Pickford, Soria, and Fraile, 1998, p. 30). Other amphicyonid species, *Cynelos euryodon* and *C. macrodon*, are represented in earlier Miocene local faunas in western Kenya and in eastern Uganda (Schmidt-Kittler, 1987). A couple taxa persist into the Pliocene in the south Asian Siwaliks. Overall, over 30 amphicyonid lesser taxa (in eight genera) are recorded in the European Miocene (Ginsburg, 1999).

There are several occurrences of pinniped Carnivora in the African upper Miocene. There are fossil representatives of Miocene Phocidae from both southernmost Africa and from the African east Mediterranean. The southern Atlantic province Langebannweg has yielded abundant remains of monachine seal, *Homiphoca* (Muizon and Hendey, 1980), specifically the species *H. capensis* (Hendey and Repenning, 1972). It is an Antarctic lobodontine seal with counterparts in the Mio-Pliocene of the American (east) coastal plain. In the south Mediterranean, monachine seals occur at Sahabi (gen. and sp. indet.) and at Wadi Natrun (*Pliophoca etrusca* Tavani), the last having a counterpart in the Italian Mediterranean.

These last occurrences are best viewed in the perspective of pinniped diversity within the Mio-Pliocene of the Paratethyan realm of west Eurasia. Overall there are eleven recognized species

of Miocene age and five species of (mostly earlier) Pliocene age in the central/eastern Paratethys (Koretsky, 2001). The taxonomic status and phylogenetic affinities among phocids remain a matter of some debate. The different perspectives are, in part, set out in Berta and Wyss (1994), Koretsky (2001), and McKenna and Bell (1997).

The taxonomic composition and attendant (species) diversity of mustelids differs very substantially between those African localities (Table 10) and those of western Eurasia. The overall (known) diversity is similar, if not identical, with about ten and thirteen or more, lesser taxa respectively. The main differences are in the dominance of Palearctic mustelines (a *Martes* is found only at Beni Mellal), melines, and mephitines in the latter region. There are partial generic overlaps (about half) between the areas in respect to several lutrines, but none at the species level; the non-overlaps of the former are instead shared with southern Asia. The mellivorines, including very large forms, are distinctively African, and presumably autochthonous. A large gulonine—*Plesiogulo*—is both African and Holarctic in distribution, in the latter instance an Asian emigrant dispersed into northern America. Almost certainly the African mustelid diversity was still greater, and regionally differentiated than presently indicated. The masked, often nocturnal behavior, and, probably, habitat specificity have constrained their appearance in local fossil faunas.

Finally, there is the issue of the Simocyoninae, accorded (by most) subfamilial status, comprising a single eponymous genus with perhaps several species. It, or the genus (or even genera) have historically been inferred to have various higher relationships or, even as Werdelin (1996) probably correctly at the time, left in limbo as “family indet.” It has come to be encompassed within Procyonidae (McKenna and Bell, 1997) or within a separate Ailuridae family (Ginsburg, 1999) according to different authors and their approach to taxonomy. However, the abundance of its relatives is within the earlier and middle Miocene, in substantial diversity and seemingly strictly Eurasiatic in distribution. Its roots are often acknowledged to lie within *Alopecocyon*, of middle Miocene age, a genus which is still insufficiently known but presumptively (only?) European in distribution. Hence *Simocyon* is acceptable as a terminal taxon of its lineage, and have extra-Eurasian dispersal into both Africa and North America.

Acknowledgments

We express our gratitude to the Office of the President, Kenya, for the authorization to conduct research in Kenya, the Masai people of the Narok District, and the Divisions of Palaeontology and Casting staff at the National Museums of Kenya. Funding was provided in part by the L.S.B. Leakey Foundation, the University of Illinois Center for African Studies and Research Board, the National Science Foundation grant SBR-BCS-0327208, and the National Science Foundation HOMINID grant Revealing Hominid Origins Initiative BCS-0321893. The authors are grateful to R. Jabbour for providing requisite dental dimensions of extant African *Genetta* species of collections in Musée Royale de l'Afrique Centrale (Tervuren, Belgium). Two insightful reviews by European colleagues were most helpful in effecting the final draft of this paper. The authors are grateful to L. Hlusko for the opportunity to deal with the carnivore remains recovered in the course of field investigations at the Lemudong'o locality. At a critical juncture J. Morales made one of us (FCH) aware of the on-going researches on Carnivora from the Cerro de Batallones-1 locality (province of Madrid) (Peigné, Salesa, et al., 2005), and notably that of the ailurid *Simocyon batalleri*, a generic assignment in revision of earlier

assignments by J. Viret initially to *Cephalogale* and, subsequently, to *Metarctos*. An earlier amphicyonid attribution of *batalleri* had led us to the inference that, as at Lothagam (and elsewhere in northern Africa) an amphicyonid was apparently also present, if not readily identifiable at Lemudong'o. Hence, on the basis of the aforesaid description and analysis, the attribution of the single Lemudong'o specimen here has been to *Simocyon* sp. indet. And, as Morales cautioned, it is not readily and certainly feasible to differentiate between upper cheek teeth of these higher taxa.

References

- Alcala-Martinez, L. 1994. Macromamíferos neógenos de la fosa de Alfambra-Teruel. Teruel Instituto de Estudios Turolenses, Museo Nacional de Ciencias Naturales, Madrid. 554 p.
- Alcala, L., P. Montoya, and J. Morales. 1994. New large mustelids from the late Miocene of the Teruel basin (Spain). *Comptes Rendus de l'Académie des Sciences, Paris, Series II, Sciences de la Terre et la Planètes*, 319:1093–1100.
- Allen, J. H. 1924. Carnivora collected by the American Museum Congo Expedition. *Bulletin of the American Museum of Natural History*, 47:73–281.
- Ambrose, S., L. J. Hlusko, D. Kyule, A. Deino, and M. Williams. 2003. Lemudong'o: a new 6 Ma paleontological site near Narok, Kenya Rift Valley. *Journal of Human Evolution*, 44:737–742.
- Barry, J. C. 1983. *Herpestes* (Viverridae, Carnivora) from the Miocene of Pakistan. *Journal of Paleontology*, 57:150–156.
- Barry, J. C. 1987. Large carnivores (Canidae, Hyaenidae, Felidae) from Laetoli, p. 235–258. In M. D. Leakey and J. M. Harris (eds.), *Laetoli: a Pliocene Site in Northern Tanzania*. Clarendon Press, Oxford.
- de Beaumont, G. 1964. Essai sur la position taxonomique des genres *Alopecocyon* Viret et *Simocyon* Wagner (Carnivora). *Eclogae Geologicae Helvetiae*, 57:829–836.
- Bernor, R. L., and P. P. Pavlakakis. 1987. Zoogeographic relationships of the Sahabi large mammal fauna (early Pliocene, Libya), p. 349–383. In N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelin, and D. D. Boaz (eds.), *Neogene Paleontology and Geology of Sahabi*. A. W. Liss, New York.
- Berta, A. 1988. Quaternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora). University of California Publications in Geological Sciences, 132:1–149.
- Berta, A., and A. R. Wyss. 1994. Pinniped phylogeny, p. 33–56. In A. Berta and T. A. Deméré (eds.), *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.*, Proceedings of the San Diego Natural History Society, 29.
- Bonaparte, C. L. J. L. 1845. *Catalogo metodico dei mammiferi europei*. Giacomo, Pirola, Milan. 36 p.
- Bowditch, T. E. 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. J. Smith. Paris. 115 + [31] p., 16 plates.
- Bryant, H. N. 1996. Explicitness stability and universality in the phylogenetic definition and usage of taxon names: a case study of the phylogenetic taxonomy of the Carnivora (Mammalia). *Systematic Biology*, 45(2):174–189.
- Chang, H. C., and L. Houyi. 1964. On specimens from *Metailurus* from Yushe, Shansi. *Vertebrata Palasiatica*, 8(2):182–186.
- Crusafont Pairó, M. 1950. El primer representante del género *Canis* en el Pontiense Eurasiático (*Canis cipio* nova sp). *Boletín de la Real Sociedad Española de Historia Natural*, Madrid, 48:43–56.
- Cuvier, G. 1816. *La règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Volume 1, Les Mammifères. Deterville, Paris. 540 p.
- Dawkins, W. B. 1868. Fossil animals and geology of Attica, by Albert Gaudry. (Critical summary). *Quarterly Journal of the Geological Society London*, 24:1–7.
- Deino, A. L., and S. H. Ambrose. 2007. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Lemudong'o late Miocene fossil assemblages, southern Kenya Rift. *Kirtlandia*, 56:65–71.
- Fischer von Woldheim, G. 1817. *Adversaria zoologica*. Mémoires Société Imperiale des Naturalistes, Moscow, 5:368–428.
- Flower, W. H. 1869. On the value of the characters of the base of the cranium in the classification of the order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. *Proceedings of the Zoological Society of London*, 1869:4–37.
- Flynn, J. J., N. A. Neff, and R. H. Tedford. 1988. Phylogeny of the Carnivora, p. 73–116. In M. Benton (ed.), *The Phylogeny and Classification of the Tetrapods*. Volume 2. Mammals. Clarendon Press, Oxford.
- Flynn, J. J., J. A. Finarelli, S. Zehr, J. Hsu, and M. A. Nedbal. 2005. Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *Systematic Biology*, 54(2):317–337.
- Flynn, J. J., and G. D. Wesley-Hunt. 2005. Carnivora, p. 175–198. In K. D. Rose and J. D. Archibald (eds.), *The rise of Placental Mammals: Origins and Relationships of the Major Extant Clades*. John Hopkins University Press, Baltimore and London.
- Garevski, R. 1974. Beitrag zur Kenntnis der Pliozänfauna macedonien. *Fragment Balcanica, Skopje (Musei Macedonici Scientiarum Naturalium Skopje)*, 9:189–197.
- Gaubert, P., C. A. Fernandes, M. W. Bruford, and G. Veron. 2004. Genets (Carnivora, Viverridae) in Africa: an evolutionary synthesis based on cytochrome b sequences and morphological characters. *Biological Journal of the Linnean Society*, 81:589–610.
- Gaubert, P., P. J. Taylor, C. A. Fernandes, M. W. Bruford, and G. Veron. 2005. Patterns of cryptic hybridization revealed by using an integrative approach: a case study on genets (Carnivora, Viverridae, *Genetta* spp.) from the South African subregion. *Biological Journal of the Linnean Society*, 86:11–33.
- Gaubert, P., P. J. Taylor, and G. Veron. 2005. Integrative taxonomy and phylogenetic systematics of the genets (Carnivora, Viverridae, *Genetta*): a new classification of the most speciose carnivoran genus in Africa, p. 371–383. In B. A. Huber, et al. (2005). *African Biodiversity*. Springer, New York.
- Gaudry, A. 1861. Note sur les carnassiers fossiles de Pikermi (Grèce). *Bulletin de la Société d'Études Géologiques de France, Series 2*, 18:527–537.
- Geoffroy Saint-Hilaire, I. 1837. Notice sur deux nouveaux genres de mammifères carnassiers, les ichneumies, du continent africain, et les gatidies, de Madagascar. *Comptes Rendus hebdomadaires des séances de l'Académie des Sciences, Paris, Series D Sciences Naturelles*, 5:578–582. [Extrait in *Annales des Sciences Naturelles, Zoologie, Paris, Series 2*, 8:249–252.]
- Geraads, D. 1989. Vertébrés fossiles du Miocène supérieur du Djebel Krechem el Artsouma (Tunisie centrale). *Comparisons biostratigraphiques*. *Géobios*, 22:777–801.
- Gill, T. 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collection*, 11(1):i–vi, 1–98.

- Ginsburg, L. 1977. Les carnivores du Miocène de Beni Mellal (Manoc). *Geologie Méditerranéenne*, 4:225–240.
- Ginsburg, L. 1999. Order Carnivora, p. 109–148. *In* G. E. Rössner and K. Heissig (eds.), *Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, Munich.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository*, 15:296–310.
- Gray, J. E. 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annales de Philosophie*, new Series, 10(whole Series 26):337–344.
- Gray, J. E. 1869. Catalogue of Carnivorous, Pachydermatous and Edentate Mammals in the British Museum (Natural History). British Museum (Natural History) Publications, London. 398 p.
- Haile-Selassie, Y. 2001. Late Miocene mammalian fauna from the Middle Awash Valley, Ethiopia. Unpublished Ph.D. dissertation, University of California, Berkeley. 425 p.
- Haile-Selassie, Y., L. J. Hlusko, and F. C. Howell. 2004a. A new species of *Plesiogulo* (Mustelidae: Carnivora) from the late Miocene of Africa. *Paleontologia Africana*, 40:85–88.
- Haile-Selassie, Y., G. WoldeGabriel, T. D. White, R. L. Bernor, D. DeGusta, P. R. Renne, W. K. Hart, E. Vrba, S. Ambrose, and F. C. Howell. 2004b. Mio-Pliocene mammals from the Middle Awash, Ethiopia. *Géobios*, 37:536–552.
- Harrison, J. A. 1981. A review of the extinct wolverine, *Plesiogulo* (Carnivora, Mustelidae), from North America. *Smithsonian Contributions to Paleobiology*, 46:1–27.
- Hendey, Q. B. 1974. The late Cenozoic Carnivora of the southwestern Cape Province. *Annals of the South African Museum*, Cape Town, 63:1–369.
- Hendey, Q. B. 1978a. Late Tertiary Hyainidae from Langebaanweg, South Africa, and their relevance to the phylogeny of the family. *Annals of the South African Museum*, Cape Town, 76:265–294.
- Hendey, Q. B. 1978b. Late Tertiary Mustelidae (Mammalia, Carnivora) from Langebaanweg, South Africa. *Annals of the South African Museum*, Cape Town, 76:329–357.
- Hendey, Q. B. 1980. *Agriotherium* (Mammalia, Ursidae) from Langebaanweg, South Africa, and relationships of the genus. *Annals of the South African Museum*, Cape Town, 81:1–109.
- Hendey, Q. B., and C. A. Repenning. 1972. A Pliocene phocid from South Africa. *Annals of the South African Museum*, Cape Town, 59:71–98.
- Howell, F. C. 1980. Zonation of late Miocene and early Pliocene circum-Mediterranean faunas. *Géobios*, 13:653–657.
- Howell, F. C. 1987. Preliminary observations on Carnivora from the Sahabi Formation (Libya), p. 153–181. *In* N. T. Boaz, A. El-Arnauti, A. W. Gaziry, J. de Heinzelin, and D. D. Boaz (eds.), *Neogene Paleontology and Geology of Sahabi*. A. R. Liss, New York.
- Howell, F. C., and G. Petter. 1980. The *Pachycrocuta* and *Hyaena* lineages/Plio-Pleistocene and extant species of the Hyainidae). Their relationships with Miocene icthitheres: *Pallyhaena* and *Hyaenictitherium*. *Géobios*, 13:579–623.
- Howell, F. C., and G. Petter. 1985. Comparative observations on some middle and upper Miocene hyainids: Genera *Percrocuta* KRETZOI; *Allohyaena* KRETZOI; *Adcrocuta* KRETZOI (Mammalia, Carnivora, Hyainidae). *Géobios*, 18:419–476.
- Hunt, R. M. J. 1996. Biogeography of the Order Carnivora, p. 485–541. *In* J. L. Gittleman (ed.), *Carnivore Behavior, Ecology, and Evolution*, Volume 2. Cornell University Press, Ithaca.
- Hunt, R. M. J. 1998. Amphicyonidae, p. 196–221. *In* C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary Mammals of North America*. Volume 1. Terrestrial Carnivores, Ungulates and Ungulate-like Mammals. Cambridge University Press, Cambridge.
- Hunt, R. M. J., and R. H. Tedford. 1993. Phylogenetic relationship within the ailuroid carnivora and implications of their temporal and geographic distribution, p. 53–73. *In* F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), *Mammal Phylogeny (Placentals)*. Springer Verlag, New York.
- Illiger, C. 1811. *Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis*. C. Salfeld, Berlin. xviii + 301 p.
- Koretsky, I. A. 2001. Morphology and systematics of Miocene Phocinae (Mammalia:Carnivora) from the Paratethys and the North Atlantic region. *Geologica Hungarica*, Series Paleontologica, Budapest, fasciculus, 54:1–109.
- Koufos, G. D. 1997. The canids *Eucyon* and *Nyctereutes* from the Ruscinian of Macedonia (Greece). *Paleontologia i Evolució*, Sabadell, 30/31:39–48.
- Kretzoi, M. 1945. Bemerkungen über das Raubtier System. *Annales Historico-Naturales Musei Nationalis Hungarici*, Budapest, 38:59–83.
- Kurtén, B. 1970. The Neogene wolverine *Plesiogulo* and the origin of *Gulo* (Carnivora, Mammalia). *Acta Zoologica Fennica*, 131:1–22.
- Kurtén, B. 1976. Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. *Notes du Service Géologique de Tunisie*, 42:177–214.
- Kurtén, B., and R. Rausch. 1959. Biometric comparisons between North American and European mammals. *Acta Arctica*, 11:1–44.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Volume 1, [ii] + 824 p. Laurentii Salvii., Stockholm.
- Lydekker, R. 1885. Catalogue of the fossil Mammalia in the British Museum (Natural History). Part 1 Primates, Chiroptera, Insectivora, Carnivora and Rodentia. British Museum (Natural History), London. 268 p.
- McKenna, M. C., and S. K. Bell. 1997. *Classification of Mammals Above the Species Level*. Columbia University Press, New York. 631 p.
- Mein, P. 1999. Miocene Mammal Chronology, p. 25–38. *In* G. E. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*. Dr. Friedrich Pfeil, München.
- Melentis, J. K. 1968. Studien über Vertebraten griechenlands. 19. Die Pkermifauna von Halmyropotamus (Euböa, Griechenland). *Annales Géologiques des Pays Helléniques*, 19: 285–404.
- Merriam, J. C. 1911a. Tertiary mammal beds of Virgin Valley and Thousand Creek in northwestern Nevada. University of California Publications in Geology, 6:199–304.
- Merriam, J. C. 1911b. Carnivora from the Tertiary formations of the John Day Region. University of California Publications in Geology, 5:479–484.
- Morales, J., and D. Soria. 1979. Nuevos datos sobre los carnívoros del área de Teruel. *Síntesis y biostratigrafía*. *Estudios Geológicos*, 35:497–540.
- Morales, J., M. Pickford, D. Soria, and S. Fraile. 1998. New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclogae Geologiae Helveticae*, 91:27–40.

- Morales, J., M. Pickford, and D. Soria. 2005. Carnivores from the Late Miocene and basal Pliocene of the Tugen Hills, Kenya. *Revista de la Sociedad Geológica de España*, 18:39–61.
- Morales, J., M. Pickford, D. Soria, and M. F. Salesa. 2004. Carnivores from the late Miocene and basal Pliocene of the Tugen Hills, Kenya. 32nd International Geological Congress, Florence, Abstracts, 380 p.
- Muizon, C. de, and Q. B. Hendey. 1980. Late Tertiary seals of the South Atlantic Ocean. *Annals of the South African Museum*, Cape Town, 82:96–128.
- Odintsov, I. A. 1967. New species of Pliocene Carnivora, *Vulpes odessana* sp. nov., from the karstic caves of Odessa. *Paleontologicheskyy Sbornik*, Lwow, 4:130–137 (in Russian).
- Parlow, M. 1914. Mammifères Tertiaires de la Nouvelle Russie. 2nd Part: Nouvelles Mémoires de la Société des Naturalistes, Moscow, 17:1–52.
- Peigné, S., L. de Bonis, A. Likus, H. T. Mackaye, P. Vignaud, and M. Brunet. 2005a. The earliest modern mongoose (Carnivora, Herpestidae) from Africa (late Miocene of Chad). *Naturwissenschaften*, 92:287–292.
- Peigné, S., L. de Bonis, A. Likus, H. T. Mackaye, P. Vignaud, and M. Brunet. 2005b. A new machairodontine (Carnivora, Felidae) from the late Miocene hominid locality of TM 266, Toros-Menalla, Chad. *Comptes Rendus Palevol*, 4:243–253.
- Peigné, S., M. F. Salesa, M. Antón, and J. Morales. 2005. Ailurid carnivoran mammal *Simocyon* from the late Miocene of Spain and the systematics of the genus. *Acta Palaeontologica Polonica*, 50:219–238.
- Petter, G. 1994. Carnivores des régions de Nkondo et de Kisegi-Nyabusosi (Rift Occidental, Ouganda), p. 207–215. In B. Senut and M. Pickford (eds.), *Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire, Volume II Paléobiologie*. Occasional Publication 1994/29, CIFEG, Orleans, France.
- Petter, G., M. Pickford, and F. C. Howell. 1991. La loutre piscivore du Pliocène de Nyaburogo et de Nkondo (Ouganda, Afrique orientale): *Torolutra ougandensis* n. g., n. sp. (Mammalia, Carnivora). *Comptes Rendus de l'Académie des Sciences*, Paris, Series II, 312:949–955.
- Petter, G., M. Pickford, and B. Senut. 1994. Présence du genre *Agriotherium* dans le Miocène terminal de la Formation de Nkondo (Ouganda, Afrique orientale). *Comptes Rendus de l'Académie des Sciences*, Paris, Series II, 319:713–717.
- Petter, G., and H. Thomas. 1986. Les Agriotheriinae (Mammalia, Carnivora) Néogènes de l'ancien monde, présence du genre *Indarctos* dans la faune de Menacer (ex-Marceau), Algérie. *Géobios*, 19:573–576.
- Pilgrim, G. E. 1931. Catalogue of the Pontian Carnivora of Europe in the Department of Geology. British Museum of Natural History, London. 174 p.
- Pons Moyà, J., and M. Crusafont Pairó. 1978. El Canis cipio Crusafont (1950), comparacion con los canidos del Plioceno y Pleistoceno europeo. *Acta Geologica Hispanica*, 13:133–136.
- Pons Moya, J. 1987. *Fortunictis* nov. gen., *acerensis* nov. sp. nuevo Metailurini (Mammalia, Carnivora) del Mioceno superior de la peninsula Ibérica. *Paleontologia i Evolució*, Sabadel, 21:63–68.
- Qiu, X. 2003. Dispersals of Neogene carnivorans between Asia and North America. *Bulletin of the American Museum of Natural History*, 279:18–31.
- Qui, Z. X., W. Wu, and Z. Qiu. 1999. Miocene mammal faunal sequence of China: palaeozoogeography and Eurasian relationships, p. 443–455. In G. E. Rössner and K. Heissig (eds.), *Miocene Land Mammal of Europe*. Verlag Dr. Friedrich Pfeil, Munich.
- Rook, L. 1992. “*Canis*” *monticinensis* sp. nov., a new Canidae (Carnivora, Mammalia) from the late Messinian of Italy. *Bollettino della Società Paleontologica Italiana*, 31:151–156.
- Rook, L. 1993. I Cani dell'Eurasia dal Miocene Superiore al Pleistocene Medio, *Estudio Paleontológico (Dottorato di Ricerca in Paleontologia)*. Università Consorziata. Modena, BolognaFirenzeRomaLa SapienzaFlorence. 131 p.
- Rook, L., G. Ficarelli, and D. Torre. 1991. Messinian carnivores from Italy. *Bollettino della Società Paleontologica Italiana*, 30:7–22.
- Rook, L., and B. Martínez-Navarro. 2004. *Viverra howelli* n. sp., a new viverrid (Carnivora, Mammalia) from the Baccinello-Cinigiano basin (latest Miocene, Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 110:719–723.
- Roth, J., and A. Wagner. 1855. Die fossilen Knochenüberreste von Pikermi in Griechenland. *Abhandlungen der mathematisch-physikalischen Classe der Königlich bayerischen Akademie der Wissenschaften*, München, 7:371–464.
- Roussiakis, S. J. 2001. *Metailarus major* Zdansky, 1924 (Carnivora, Mammalia) from the classical locality of Pikermi (Attica, Greece). *Annales de Paleontologie*, 87:119–132.
- Roussiakis, S. J. 2002. Mustelids and feloids (Mammalia, Carnivora) from the late Miocene locality of Pikermi (Attica, Greece). *Géobios*, 35:699–719.
- Schlosser, M. 1887–1890. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs, und deren Beziehungen zu ihren lebenden und fossilen aussereuropäischen Verwandten. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und der Orients*, 6:1–493. Carnivora p. 225–450, plates V–IX.1.
- Schmidt-Kittler, N. 1981. Sur Stammesgeschichte der mardenverwandten Raubtiergruppen (Musteloidea, Carnivora): *Ecologiae Geologicae Helvetiae*, 74:753–801.
- Schmidt-Kittler, N. 1987. The Carnivora (Fissipedia) from the Lower Miocene of East Africa. *Paleontographica A*, 197:85–126.
- Semenov, Y. A. 1989. Ictitheres and morphologically related hyaenas of the Neogene of the USSR. *Naukova Dumka*, Kiev. 179 p. (in Russian)
- Severson, M. N. 1859. Notice sur la classification multisériale des Carnivores, spécialement des félidés, et les études zoologie générale qui sy rattachent. *Révue et Magazine de la Zoologie*, Paris, Series 2, 10:385–393.
- Shotwell, J. A. 1970. Pliocene mammals of southwest Oregon and adjacent Idaho: Museum of Natural History, University of Oregon, Eugene, Bulletin, 17:1–103.
- Sickenberg, O. 1972. Ein Unterkiefer des Caniden *Nyctereutes* (DEP.) aus der Umgebung von Saloniki (Griech-Mazedonien) und seine biostratigraphische Bedeutung. *Annalen Naturhistorischen Museum Wien*, 76:499–513.
- Slattery, J. P., and S. J. O'Brien. 1995. Molecular phylogeny of the red panda (*Ailurus fulgens*). *Journal of Heredity*, 86:413–422.
- Steininger, F. F. 1999. Chronostratigraphy, geochronology and biochronology of the Miocene “European Land Mammal Mega-Zones” (ELMMZ) and the Miocene “Mammal-Zones (MN-Zones),” p. 9–24. In G. E. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*. Dr. Friedrich Pfeil, München.

- Stromer, E. 1931. Reste süßwasser und landbewonender Wirbeltiere aus den Diamantfeldern Klein-Namaqualandes (Südwestafrika). Sitzungsberichte der Mathematisch-naturwissenschaftlichen Abteilung der Bayerischen Akademie der Wissenschaften zu München, 1931:17–47.
- Swainson, W. 1835. On the natural history and classification of quadrupeds, *In* The Cabinet Cyclopaedia, Conducted by the Rev. Dionysis Lardner. Longman, Rees, Orme (etc.), London. viii + 397 p.
- Tedford, R. H. 1976. Relationships of pinnipeds to other Carnivora (Mammalia). *Systematic Zoology*, 25:363–374.
- Tedford, R. H., and Z.-X. Qiu. 1996. A new canid genus from the Pliocene of Yushe, Shanxi province. *Vertebrata Palasiatica*, 34:27–40.
- Tedrow, A. R., J. A. Baskin, and S. F. Robinson. 1999. An additional occurrence of *Simocyon* (Mammalia, Carnivora, Procyonidae) in North America. *In* D. D. Gillette (ed.), *Vertebrate Paleontology in Utah*, Utah Geological Survey, Miscellaneous Publication 99-1: 487–493.
- Teilhard de Chardin, P., and P. Leroy. 1945. Les Félicés de Chine. Institut de Géobiologie, Peking, 58 p.
- Thenius, E. 1949. Zur Herkunft der *Simocyoniden* (Canidae, Mammalia). Sitzungsberichte der Österreichische Academie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Wien, part 1, 158:799–810.
- Thomas, H., and G. Petter. 1986. Révision de la faune de mammifères du Miocène supérieur de Menacer (ex-Marceau), Algerie: discussion sur l'âge du gisement. *Géobios*, 19:357–373.
- Thorpe, M. R. 1921. Two new fossil Carnivora. *American Journal of Science*, 1:477–483.
- Thorpe, M. R. 1922. *Araeocyon*, a probable Old World migrant. *American Journal of Science*, 3:371–377.
- Trouessart, E. L. 1885. Catalogue des mammifères vivants et fossiles. Carnivores, *Bulletin de la Société Études Sciences Angers*, 14:1–108.
- Villalta, J. F. de., and M. Crusafont. 1943. Los vertebrados del Mioceno continental de la cuenca del Vallés Penedés (provincia de Barcelona) I. Insectivoros. II. Carnivoros. *Buletin del Instituto de Geologia y Mineralogia de España*, Series 3, 56:147–336.
- Villalta, J. F. de., and M. Crusafont. 1948. Neuvos aportaciones al conocimiento de los carnivores pontienses del Vallés Penedés. *Publicaciones del Instituto de Geologia de Barcelona*, 7(Part 1. Miscelánea Almeria):81–121.
- Viret, J. 1929. Cephalogale batalleri carnassier du Pontien de Catalogne. *Bulletin de la Société d' Histoire Naturelle de Toulouse*, 58:567–568.
- Viranta, S. 1996. European Miocene Amphicyonidae—taxonomy, systematics and ecology. *Acta Zoologica Fennica*, no. 204. 61 pages.
- Wagner, A. 1857. Neue Beiträge sur Kenntniss der fossilen Säugetier—Überreste von Pikermi. *Abhandlungen der mathemat-physikalischen Classe der königlich Bayerischen Akademie der Wissenschaften, München*, 8:111–158.
- Wagner, A. 1858. Geschichte der Urwelt, mit besonderer Berücksichtigung der Menschenrassen und des mosaichen Schöpfungsberichtes (Zweite Auflage). Leopold Voss, Leipzig. 528 p.
- Wagner, A. 1885. Geschichte der Urwelt, Second edition. Leopold Voss, Leipzig. 528 p.
- Wang, X. 1997. New cranial material of *Simocyon* from China, and its implications for phylogenetic relationship to the red panda (*Ailurus*). *Journal of Vertebrate Paleontology*, 17:184–198.
- Wang, X., R. H. Tedford, and B. E. Taylor. 1999. Phylogenetic systematics of the Borophaginae (Carnivora: Canidae). *Bulletin of the America Museum of Natural History*. 243. 391 p.
- Werdelin, L. 1996. Carnivores, exclusive of Hyaenidae, from the later Miocene of Europe and western Asia, p. 271–289. *In* R. L. Bernor, V. Fahlbusch, and W. Mittmann (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York.
- Werdelin, L. 2003a. Mio-Pliocene Carnivora from Lothagam Kenya, p. 261–328. *In* M. G. Leakey and J. M. Harris (eds.), *Lothagam: The Dawn of Humanity in Eastern Africa*. Columbia University Press, New York.
- Werdelin, L. 2003b. Carnivora from the Kanapoi hominid site, Turkana basin, northern Kenya. *Contributions in Science, Natural History Museum of Los Angeles County*, 498:115–132.
- Werdelin, L., and M. E. Lewis. 2000. Carnivora from the South Turkwell hominid site, northern Kenya. *Journal of Paleontology*, 74:1173–1180.
- Werdelin, L., and N. Solounias. 1991. The Hyaenidae: taxonomy, systematics and evolution: *Fossils and Strata*, 30:1–104.
- Werdelin, L., and N. Solounias. 1996. The evolutionary history of hyaenas in Europe and western Asia during the Miocene, p. 290–306. *In* R. L. Bernor, V. Fahlbusch, and H.-W. Mittman (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York.
- Werdelin, L., A. Turner, and N. Solounias. 1994. Studies of fossil hyaenids: the genera *Hyaenictis* Gaudry and *Chasmaportetes* Hay, with a reconsideration of the Hyaenidae of Langebaanweg, South Africa. *Zoological Journal of the Linnean Society*, 111:197–217.
- Wilson, D. E., and D. M. Reeder. 1993. *Mammal Species of the World: A Taxonomic and Geographic Reference*. Second Edition. Smithsonian Institution Press, Washington and London. 1207 p.
- Wolsan, M. 1993. Phylogeny and classification of early European Mustelida (Mammalia: Carnivora). *Acta Theriologica*, 38: 345–384.
- Wozencraft, W. C. 1993. Order Carnivora, p. 279–348. *In* D. E. Wilson and D. M. Reeder (eds.), *Mammal Species of The World*. Smithsonian Institution Press, Washington, D. C.
- Wyss, A. R., and J. J. Flynn. 1993. A phylogenetic analysis and definition of the Carnivora, p. 32–52. *In* F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), *Mammal Phylogeny. Placentals*. Springer-Verlag, New York.
- Zdansky, O. 1924. Jungtertiäre Carnivoren chinas. *Paleontologica Sinica*, Series C, 2:1–149.