The last amphicyonid
(Mammalia, Carnivora) in Africa

Lars WERDELIN
Swedish Museum of Natural History, Department of Palaeozoology,
Box 50007, SE-104 05 Stockholm (Sweden)
werdelin@nrm.se

Scott W. SIMPSON
Case Western Reserve University – School of Medicine,
Department of Anatomy,
10900 Euclid Avenue, Cleveland, OH 44106-4930 (USA)
sws3@cwru.edu

ABSTRACT

KEY WORDS
Mammalia,
Carnivora,
Amphicyonidae,
Neogene,
Miocene,
Africa,
Ethiopia,
Kenya,
new genus,
new species.

Amphicyonidae are a common element of carnivoran faunas in the early and middle Miocene of Eurasia and North America, but by the Messinian they had become extinct there, except possibly on the Indian subcontinent. In Africa, amphicyonids are poorly known from a scattering of records from the late Oligocene to the late Miocene. In this paper, we describe the last-surviving amphicyonid in Africa, from Messinian-age sediments (dated *c.* 6.5-5.3 Ma) of Ethiopia (Gona) and Kenya (Lothagam and possibly Lemudong'o). This new taxon shows unique adaptations to hypercarnivory in the lower molars and was small for an amphicyonid, dentally about the size of a coyote, *Canis latrans*.

RÉSUMÉ

Le dernier amphicyonidé (Mammalia, Carnivora) en Afrique.

MOTS CLÉS
Mammalia,
Carnivora,
Amphicyonidae,
Néogène,
Miocène,
Afrique,
Éthiopie,
Kenya,
genre nouveau,
espèce nouvelle.

Les Amphicyonidae sont des éléments courants dans les faunes de carnivores du Miocène inférieur et moyen d'Eurasie et d'Amérique du Nord, où ils s'éteignent avant le Messinien, à l'exception peut-être du sous-continent indien. En Afrique, les amphicyonidés sont peu connus, avec un petit nombre de sites de l'Oligocène supérieur au Miocène supérieur. Dans cet article, nous décrivons le dernier survivant des amphicyonidés en Afrique, de sédiments d'âge messinien (daté d'environ 6,5-5,3 Ma) d'Éthiopie (Gona) et du Kenya (Lothagam et peut-être Lemudong'o). Ce nouveau taxon montre des adaptations hypercarnivores tout à fait particulières sur les molaires inférieures et était relativement petit pour un amphicyonidé, ses dents ayant la taille de celles du coyote *Canis latrans*.

INTRODUCTION

The fossil record of Amphicyonidae in Africa is, to say the least, patchy and difficult to interpret. The earliest records may be an isolated incisor from Malembe, Cabinda Province, Angola, possibly of late Oligocene age (Hooijer 1963) and fragmentary remains from Moroto II, Uganda (earliest Miocene, > 20 Ma), referred by Pickford *et al.* (2003) to ?*Cynelos* sp. However, the earliest well-preserved remains of amphicyonids are from the early Burdigalian (*c.* 20 Ma) of eastern and southern Africa. Savage (1965) described two species of amphicyonid from eastern African sites that he referred to the new genus *Hecubides*: *H. euryodon* Savage, 1965 and *H. macrodon* Savage, 1965. The former is known from a series of localities, including Songhor, Rusinga, Chamtwara, Mfwangano, and Napak, all dated from the early Burdigalian to the early Langhian. The latter species, which as the name implies differs by being larger, is known from fewer localities, including Rusinga, Kalodirr, and Kipsaraman. Schmidt-Kittler (1987) noted that Savage had emphasized similarities between his *Hecubides* Savage, 1965 and the European amphicyonid *Cynelos lemanensis* (Pomel, 1846), and synonymized *Hecubides* under the latter generic name. Recently, Morales *et al.* (2007) proposed resurrecting *Hecubides* as distinct from *Cynelos* Jourdan, 1862. However, the differences are slight and as the material is limited and *Cynelos* itself in dire need of revision, we shall not here use the name *Hecubides* for these taxa.

Morales *et al.* (2008) have recently reviewed the carnivore fossil record of the lower Miocene localities in the Sperrgebiet of southern Namibia. These sites are approximately coeval with the oldest sites including *C. euryodon* (Savage, 1965) in eastern Africa. Several of these Namibian sites have yielded remains of amphicyonids, which Morales *et al.* (2008) have referred to the genus *Ysengrinia* Ginsburg, 1965, well known from the lower Miocene of western Europe and elsewhere. *Ysengrinia* is also known from the slightly younger (middle Burdigalian) locality of Arrisdrift in Namibia, in the form of the species *Y. ginsburgi* Morales, Pickford, Soria & Fraile, 1998. Arrisdrift also records the presence of a second amphicyonid, referred by Morales *et al.* (1998) to *Amphicyon giganteus* (Schintz, 1825).

Unlike the medium or small (for Miocene amphicyonids) species of *Cynelos*, the Namibian material is very large. A further very large Burdigalian amphicyonid, is known from the eastern African localities of Buluk and Fejej, but this material has yet to be described.

North Africa, too, has Burdigalian amphicyonids, in the form of cf. *Amphicyon giganteus* and the aberrant *Afrocyon burolleti* Arambourg, 1961 from Jebel Zelten, Libya and a recently described *Cynelos* sp. from Wadi Moghara, Egypt (Morlo *et al.* 2007). The relationships of *A. burolleti* to other African amphicyonids, as well as to other Amphicyonidae in general, are obscure.

The middle Miocene (Langhian and Serravallian) amphicyonids of Africa are more restricted, both in terms of number of records and in their taxonomic affinities. Due to a dearth of localities, there are no southern African amphicyonids from this time period, but representatives of the family have been found in both eastern and North Africa. All of these have been referred to the genus *Agnotherium* Kaup, 1833. In eastern Africa, *A. kiptalami* Morales & Pickford, 2005 has been reported from Kabarsero, Ngorora Formation, Member D (Morales & Pickford 2005a). A related, undescribed form is known from Fort Ternan (Morales & Pickford 2005a). In North Africa, fragmentary remains tentatively referred to the European species *A. antiquum* Kaup, 1833 have been reported (Kurtén 1976; Ginsburg 1977). All of these forms are of medium size.

In the Upper Miocene, finally, amphicyonids are somewhat better represented, though this may simply be an effect of a greater number of localities, coupled with the longer time span of the upper Miocene compared to the middle Miocene. North Africa records another aberrant form from the Tortonian of Oued Mya 1, Algeria, *Myacyon dojambir* Sudre & Haretenberger, 1992, of uncertain affinities (Sudre & Hartenberger 1992). A probably somewhat younger Tortonian form has been reported from the Namurungule Formation, Samburu Hills (described as Ursidae or Amphicyonidae by Tsujikawa [2005], but clearly of amphicyonid affinities; cf. Werdelin & Peigné [in press]). Both of these are large species.

The youngest African amphicyonids are of Messinian age. Werdelin (2003) reported fragmentary remains of a large amphicyonid, recorded only as Amphicyonidae sp. A, but with general similarities to *Amphicyon* sp., from the lower Nawata Formation, Lothagam, Kenya. Another amphicyonid is recorded from Toros-Menalla in Chad (Peigné *et al.* 2008). However, the youngest amphicyonid material thus far described from Africa comes from the Upper Nawata Formation, Lothagam, in the form of a broken mandibular ramus with damaged m1 and alveoli for m2 and m3 described as Amphicyonidae sp. B (Werdelin 2003). Additional material that can be referred to this taxon has now been recovered and forms the subject of this contribution.

MATERIAL AND METHODS

The material described herein comes from several eastern African localities. Material from Gona is housed in the National Museum of Ethiopia, Addis Ababa (NME). Material from Lothagam and Lemudong'o is housed in the Department of Paleontology, Kenya National Museums, Nairobi (KNM). Comparative material of *Cynelos euryodon* and *C. macrodon* (Savage, 1965) is housed in the Kenya National Museums, in the Uganda Museum, Kampala (UM), and in the Department of Palaeontology, The Natural History Museum, London (BMNH). Measurement data on these specimens is either original or from the publications of Savage (1965) and Schmidt-Kittler (1987). Additional measurement data on comparative material of the European amphicyonid species *Cynelos lemanensis*, *C. helbingi* (Dehm, 1950), *C. schlosseri* (Dehm, 1950), and *C. rugosidens* (Schlosser, 1899) were generously provided by Dr Stéphane Peigné.

Measurements used are Lm1: greatest mesiodistal length of m1; Wm1: greatest buccolingual width of trigonid of m1; Lm2: greatest mesiodistal length of m2; Wm2: greatest buccolingual width of m2; LM1: greatest mesiodistal length of M1; WM1: greatest buccolingual width of M1 normal to LM1; LM2: greatest mesiodistal length of M2; WM2: greatest buccolingual width of M2 normal to LM2. All measurements are in millimetres. Ltm1: mesiodistal length of trigonid of m1.

Standard bivariate techniques are used in the quantitative analyses. Regressions are major axes and confidence ellipses of comparative samples are all 95%. All analyses and plots were done in Aabel, ver. 2.4.2.

SYSTEMATICS

Order CARNIVORA Bowdich, 1821
Family AMPHICYONIDAE Haeckel, 1866

Genus *Bonisicyon* n. gen.

TYPE SPECIES. — *Bonisicyon illacabo* n. sp. by present designation

ETYMOLOGY. — In honour of Dr Louis de Bonis in recognition of his many contributions to the study of fossil carnivores.

DIAGNOSIS. — As for type species.

Bonisicyon illacabo n. sp.
(Fig. 1A-F)

Amphicyonidae sp. B – Werdelin 2003.

Simocyon sp. — Howell & García 2007: 124.

HOLOTYPE. — HMD1/P11 from Gona, Ethiopia, right m1. Fig. 1A-C herein (NME).

ETYMOLOGY. — From the Afar *illacabo*, end (as in "the end of the story"), a noun in apposition. The last syllable is stressed.

GEOGRAPHICAL RANGE. — Eastern Africa (Ethiopia, Kenya).

STRATIGRAPHIC RANGE. — Latest Miocene, *c.* 6.5-5.3 Ma (Messinian; ~MN13 equivalent).

LOCALITIES. — Hamadi Das (HMD), Escarpment (ESC), and ?Asbole Dora (ABD), Gona (Ethiopia), Upper Nawata Formation, Lothagam (Kenya), ?Lemudong'o (Kenya).

MATERIAL EXAMINED. — Gona (Afar Autonomous Region, Ethiopia): HMD1/P11, isolated right m1 (holotype); ESC2/P224, isolated left m2; ABD1/P35, damaged right M2. Lothagam (Turkana District, Kenya): KNM-LT 23944, a partial right horizontal ramus with roots of p4, a broken m1, the alveolus for m2 and the anterior part of the alveolus for m3; Lemudong'o (Narok District, Kenya): KNM-NK 45780, isolated left M1.

DIAGNOSIS. — Amphicyonidae of small size; carnassial shear on m1 entirely mesiodistal; m1 hypoconid formed into elongated crest, separated from trigonid by a narrow postvallid notch and effectively a part of the carnassial shear; m1 metaconid in evidence only as a bulge on the lingual side of the protoconid; m1 relatively wide and bulbous at the base of the crown; m2 broad and short.

DESCRIPTION

Material referred to Bonisicyon illacabo *n. sp.*
HMD1/P11, right m1 (Fig. 1A-C). This specimen is a very well preserved right m1. There is some sediment clinging to the specimen in places, but otherwise the preservation is pristine. The tooth is robust, with a trigonid that is about twice the length of the talonid. The mesial root is broken about 5 mm below the crown, but otherwise the tooth is complete. It is nearly unworn, with only some blunting of the apices of the main cusps. The widest part of the tooth is just mesial to the apex of the hypoconid. Mesial to this point the tooth is nearly equally wide until just mesial to the base of the metaconid remnant, then it tapers to the carnassial notch, where there is an in-turning on the lingual side, then is equally wide until just mesial to the paraconid apex, mesial to which it tapers rapidly but smoothly to the mesialmost point of the tooth. Distal to the widest point the tooth tapers gradually in width to the distal end of the hypoconid, then tapers abruptly but smoothly to the distal end of the tooth.

The trigonid consists of a well-developed paraconid and protoconid, and a metaconid that has been reduced to little more than a bump on the lingual face of the protoconid. The mesial face of the paraconid slopes almost vertically down to the mesialmost point of the tooth, which is just dorsal to the crown/root juncture. The paraconid cristid is very short and the paraconid is much lower than the protoconid and even lower than the point where the (almost entirely reduced) metaconid apex joins with the protoconid. The carnassial notch is acute but not very deep. The protoconid is tall and mesiodistally longer than the paraconid. The preprotocristid is well developed and is slightly expanded dorsally about midway between the apex of the tooth and the carnassial notch. The postprotocristid is much more vertically oriented than the preprotocristid and meets the talonid at what can only be termed a

posterior carnassial notch. Carnassial shear is almost entirely mesiodistal, with only a very slight angle between paraconid and protoconid. As noted, the metaconid is almost entirely reduced. It can best be discerned in its distal part, where it is partially separated from the protoconid by a shallow groove. No cristids are developed on the metaconid.

The talonid is entirely dominated by the hypoconid, which is almost as long as the protoconid and located directly distal to it. It is elongated into a cristid that runs the entire length of the talonid, ending with a nearly vertical face that drops to the distal end of the tooth. The hypoconid is about ⅔ the height of the protoconid. The lingual part of the talonid consists of a lingual cristid that includes what are probably poorly developed entoconid and entoconulid. This cristid is separated from the hypoconid by a narrow, shallow groove.

The anterior root is broken, as noted. At the crown level the two roots are about equally long mesiodistally, with the posterior perhaps slightly longer. There is no basal cingulum, merely a modest out-bulging of the enamel.

Lm1: 18.9; Wm1: 9.7; Ltm1: 12.0.

ESC2/P224, isolated left m2 (Fig. 1D-F). This tooth has been subjected to considerable chemical weathering, and hence the preservation is less favorable than that of the previous specimen. The specimen is coated with white residue of this process and is considerably pitted. Although the cuspids appear relatively unworn, it is not possible to state with certainty whether this is the case or whether some moderate wear is present.

The m2 is a rounded rectangle in occlusal view, with the distal end tapering more than the mesial, which is cut-off in a slightly oblique line from buccal (mesialmost) to lingual. The trigonid consists of a protoconid and metaconid with no hint of of a paraconid. The protoconid is the tallest trigonid cuspid and has distinct pre- and postcristids. The metaconid is not developed into a cuspid, but forms a low crest along the lingual side of the tooth. The enamel bulges basally on the buccal side below the protoconid but not on the lingual side below the metaconid. The area between the two trigonid cuspids forms a shallow valley but no basin.
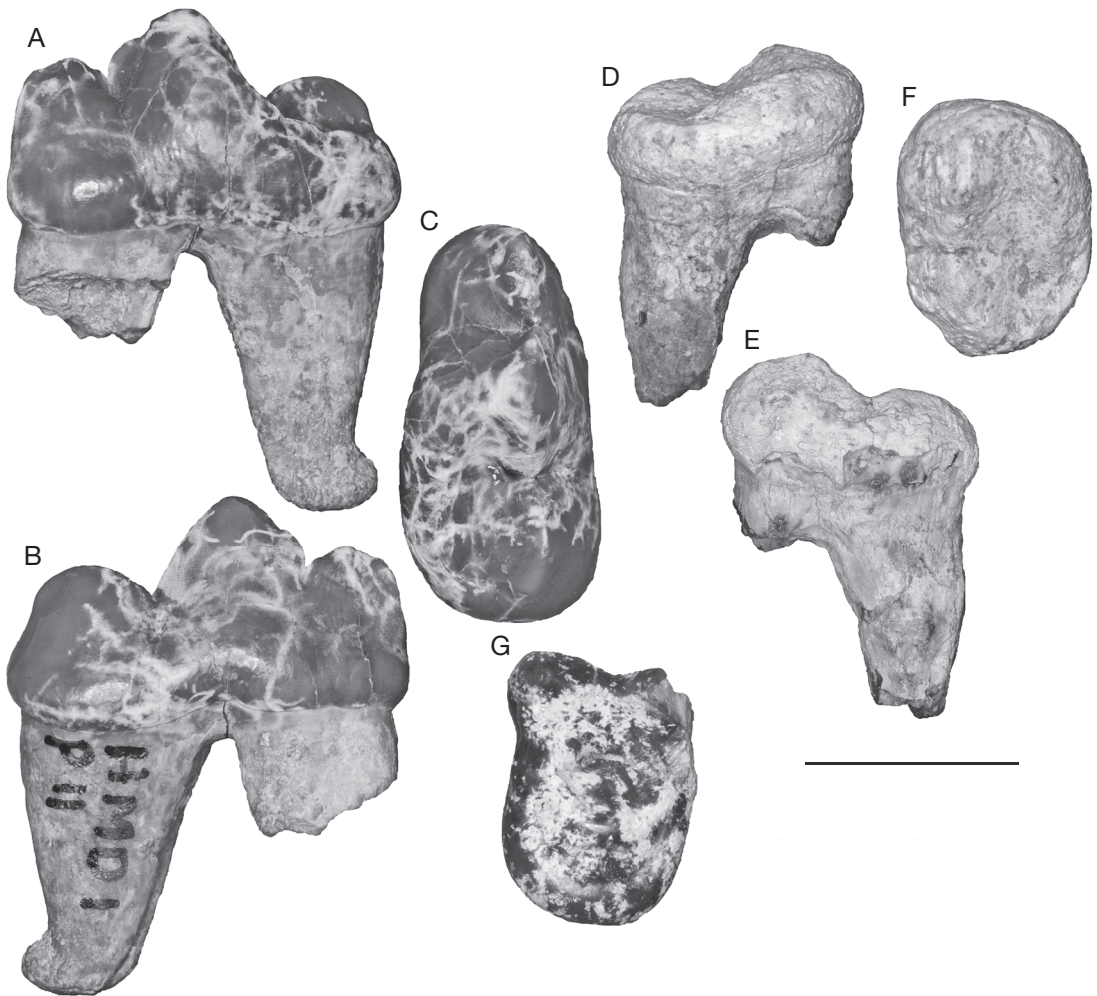
FIG. 1. — Molars of *Bonisicyon illacabo* n. gen, n. sp.: **A-C**, HMD-1-P11 (holotype), right m1, Hamadi Das, Gona, Ethiopia; **D-F**, ESC-2-P224, left m2, Escarpment, Gona, Ethiopia; **G**, ABD-1-P35, damaged right M2, Asbole Dora, Gona, Ethiopia; **A**, **D**, lingual views; **B**, **E**, buccal views; **C**, **F**, **G**, occlusal views. Scale bar: 10 mm.

The buccal bulge of the enamel continues on to the talonid beneath the hypoconid. The latter is large and crest-like and separated from the protoconid by a shallow valley but no distinct postvallid notch. There is no entoconid and the lingual half of the talonid is formed into a shallow, nearly flat basin.

As in the case of the m1 the anterior root is broken and the posterior nearly complete. The posterior root appears to have been much the larger of the two.

Lm2: 12.4; Wm2: 9.4.

KNM-LT 23944, a partial right mandibular corpus with broken m1 (after Werdelin 2003: fig. 2): the ramus is long and relatively slender. It is both deepest and thickest beneath the m1 talonid. The ramus is broken anteriorly at the anterior end of the anterior root of p4 and posteriorly just at the point where the horizontal ramus begins to ascend to the coronoid process. The latter break continues posteroventrally and the ventral half of the ramus is about 30 mm longer than the dorsal half. Posterior to m2 the ramus becomes noticeably thinner.

The anterior end of the masseteric fossa can be felt by tactile inspection rather than seen and lies posterior to the tooth row. The fourth lower premolar was a relatively short and probably quite slender tooth. The lower carnassial is short, with the talonid making up about one third of the total length of the tooth. The trigonid is relatively short given the size of the ramus. Neither trigonid cuspid can be clearly distinguished because of a strong, nearly horizontal wear facet that runs from the mesial end of the trigonid to the distal end of the talonid. The talonid has a single, well-developed and probably trenchant cuspid. There is no buccal cingulum, only a slight marginal swelling at the talonid. The m2 was, to judge from the alveoli, a broad tooth of about 14 mm length. The m3 alveolus is much smaller than either alveolus of m2.

Material referred to cf. Bonisicyon illacabo *n. sp.*
KNM-NK 45780, isolated left M1 (Howell & García 2007: fig. 3). The crown of this complete tooth is a triangle that is pinched in the center, about level with the buccal end of the preprotocrista. The trigon has three cusps. The largest is the paracone, which is a substantial, pyramidal tooth with distinct pre- and postparacristae. The metacone, though still a substantial cusp, is more crest-like. It has a short premetacrista and a longer postmetacrista. These two cusps are bounded mesially, buccally, and distally by a cingulum that is broad mesially and tapers gradually to the distal end, where the postmetacrista nearly reaches the distal margin of the tooth. The protocone is a low crescent with substantial pre- and postprotocristae. The space between the trigon cusps is deep but not formed into a flat basin. Lingually, the protocone has crenelated enamel and descends gradually to a broad cingulum that is largest centrally and tapers both mesially and distally.

LM1: 13.4; WM1: 16.9 (after Howell & García 2007).

ABD-1-P35, damaged right M2 (Fig. 1G). The tooth is missing the parastyle and a part of the paracone and paracrista. Much of the morphology of the preserved parts of the tooth is obscured by white weathering residue clinging to the occlusal surface. In occlusal outline the tooth as preserved is rectangular. It might be expected that the parastyle would have extended mesially beyond the mesial cingulum. The general relief of the tooth is low. It has three trigon cusps, a low paracone, a very low metacone, and a low protocone that forms a blunt ridge together with the pre- and postprotocristae. The metastyle is well developed and is surrounded by a cingulum. The crown buccal to the protocone forms a broad shelf with low-lying area followed buccally by a broad buccal cingulum.

WM2 at level of protocone: *c.* 11.

COMPARATIVE ANALYSIS

Ideally, the affinities and antecedents of *Bonisicyon* n. gen. would be resolved by a cladistic analysis of relationships. However, since all the material available consists of isolated teeth or, in the case of the Lothagam specimen, of a damaged mandibular corpus with a single broken tooth, very few characters are available on which such an analysis could be based. The character matrix on which Peigné *et al.* (2008) based their study of *Magericyon* Peigné, Salesa, Antón & Morales, 2008, for example, includes only three of 18 characters that can be coded in the available material of *Bonisicyon* n. gen. Thus, establishing a framework for a cladistic analysis is not possible unless more complete material becomes available in the future, and instead we have carried out a traditional comparative analysis to try to estimate the position of *Bonisicyon* n. gen. relative to other Amphicyonidae.

Morphological comparisons
The m1 with low paraconid, tall protoconid, and talonid dominated by a large hypoconid and broad almost nonexistent entoconid set on a posterolingual talonid shelf, the m2 with hypoconid as the only talonid cusp, formed into a low crest, the presence of an m3, the M1 with subtriangular shape and broad cingulum shelf surrounding the lingual margin of the tooth, all indicate that these specimens belong to the Amphicyonidae. The only other possible taxonomic allocation would be, as suggested by Howell & García (2007), to *Simocyon* Wagner,

1858. However, the M1 of *Simocyon*, though similar to that of generalized Amphicyonidae (and the Lemodung'o specimen described above), differs in several respects, even taking into account structural evolution within the *Simocyon* lineage. In the latter taxon the metacone has a less developed postmetacrista and a more developed metaconule (in *S. primigenius* Roth & Wagner, 1854 in some cases also a paraconule: Wang 1997: fig. 7 top). In the M1 from Lemudong'o, these features are developed as in typical Amphicyonidae. Setting the paracone-metacone pair as the horizontal, the mesial face of M1 in *Simocyon* tapers mesiodistally to the lingual-most point of the tooth, which is distinctly distal to the tooth midline. In the Lemudong'o specimen the mesial face of the tooth is nearly parallel to the distal face, both tapering gradually to the lingual-most point, which is set close to the tooth midline. In *Simocyon*, the protocone is set much closer to the mesial face of the tooth than to the distal face (cf. Werdelin 2005: text-fig. 3G), in the Lemudong'o specimen the protocone is set near the middle of the tooth. In *Simocyon*, the lingual cingulum extends distolingually, but is excluded from the mesial face of the tooth by the protocone. In the Lemudong'o specimen the lingual cingulum runs around the entire lingual side of the tooth without interruption from the protocone. In all these features the Lemudong'o tooth is of typical amphicyonid morphology and can positively be identified as belonging to that family. Its size matches perfectly with that of the m1 and m2 from Gona and it is reasonable to infer that they belong to the same taxon, especially given the rarity of small-medium Amphicyonidae in the African late Miocene fossil record. Since any similarities between the mandibular dentition described above and that of *Simocyon* are entirely due to plesiomorphy, we can conclude that the material truly belongs in the Amphicyonidae.

It thus remains to determine the taxonomic status and phylogenetic position of the described material, if at all possible. As noted, the fossil record of Amphicyonidae in Africa is poor and irregular, while the fossil record of Amphicyonidae in the late Miocene globally is very poor. In Europe and North America, only a handful of amphicyonids occur in the late Miocene, and by *c.* 9 Ma they had become extinct on those continents (Viranta 1996; Hunt 2002). In Asia, specifically the Indian subcontinent, the family survives longer, however. In the Siwaliks of India and Pakistan, amphicyonids are known from probably Messinian (< 7.4 Ma) levels (Pilgrim 1932; Barry *et al.* 1982; Peigné *et al.* 2006). Peigné *et al.* (2006) refer these forms to *Amphicyon lydekkeri* Pilgrim, 1910 and *Amphicyon palaeindicus* Lydekker, 1876, though their generic affinities may require revision. What is clear, is that these latest Asian amphicyonids are large forms, either identical or similar to *Amphicyon*. Thus, they are quite different from, and can have nothing to do with, *Bonisicyon illacabo* n. gen., n. sp.

Judging by the later Miocene evolution of Amphicyonidae on the northern continents, then, it is more than likely that *Bonisicyon illacabo* n. gen., n. sp. is a true African endemic, derived from African antecedents that migrated to the continent in the early or middle Miocene. The African fossil record, briefly reviewed above, includes only a handful of amphicyonid genera. Of these, *Amphicyon*, *Ysengrinia*, and *Myacyon* Sudre & Hartenberger, 1992 can immediately be excluded from any relationship with *Bonisicyon* n. gen. The former two have a more crushing dentition with shorter cutting blade, well-developed metaconid, and longer talonid on the m1 and broader upper molars with larger buccal cusps. *Myacyon* has a very peculiar m1 with shallow carnassial notch that is quite different from the m1 of any other amphicyonid. *Afrocyon*, on the other hand, has some features that are reminiscent of *Bonisicyon* n. gen. in the m1, especially the more reduced metaconid than in, e.g., *Amphicyon*, as well as the relatively short talonid. However, *Afrocyon*, like *Amphicyon*, *Ysengrinia*, and *Myacyon,* is a much larger animal and has an elongated m2 quite different in proportions from that of *Bonisicyon* n. gen., and a very tall and relatively transversely thin mandibular ramus quite unlike that of the *Bonisicyon* n. gen. specimen from Lothagam.

The two remaining amphicyonid genera with which *Bonisicyon* n. gen. may share affinities are *Cynelos* and *Agnotherium*. As noted above, the latter genus is known from the middle Miocene of North and eastern Africa. The North African finds have been referred to *Agnotherium* cf. *antiquum* Kaup, 1833

and are comparable in size and morphology to this European species. The eastern African *A. kiptalami* is similar in size to *A. antiquum* but differs in several features of the skull and dentition, such as the less developed upper carnassial blade and the apparently shorter snout (Morales & Pickford 2005). Nevertheless, the two are quite close. The youngest eastern African, and the material that is closest in size to *Bonisicyon illacabo* n. gen., n. sp. consists of three isolated teeth from Fort Ternan (*c.* 14 Ma). These teeth, m1, P4 and M1, are intermediate in size between *A. kiptalami* and *Bonisicyon* n. gen. and their morphology, particularly that of P4 and M1 clearly identifies them as belonging to a small species of *Agnotherium* (Morales & Pickford 2005). However, the morphology of the comparable teeth, m1 and M1, differs completely from *Bonisicyon* n. gen.

In Fort Ternan *Agnotherium* the m1 paraconid is relatively short and low, with highly developed pre- and postparacristids (Fig. 2). In *Bonisicyon* n. gen. the paraconid is relatively taller and more bulbous but not so trenchant. The protoconid of Fort Ternan *Agnotherium* is very tall, with a sharply pointed apex and very sharp pre- and postprotocristids. In *Bonisicyon* n. gen. the protoconid is lower and blunter. In Fort Ternan *Agnotherium* the metaconid is an individualized cuspid set at the distolingual corner of the protoconid and extending distally to form the distalmost point of the trigonid. It is a small, sharp cuspid. In *Bonisicyon* n. gen. the metaconid has been reduced to a bulge on the lingual face of the protoconid and is not an individuated cuspid at all. The talonid is broken just posterior to the apex of the hypoconid in the Fort Ternan *Agnotherium*, but what remains indicates that the hypoconid was tall and sharp, not an elongated crest as in *Bonisicyon* n. gen.

The Fort Ternan *Agnotherium* M1 is damaged and abraded, but what is left differs from the referred *Bonisicyon* n. gen. specimen from Lemudong'o in the rounded and very tall paracone and metacone and the relatively more slender lingual shelf incorporating heavily worn protocone and a small protoconulid just lingual to the paracone.

Given all these differences, we can exclude *Agnotherium* from the ancestry of *Bonisicyon* n. gen.

The last African amphicyonid genus to consider is *Cynelos* despite the extensive temporal gap between it and *Bonisicyon* n. gen.; the youngest known *Cynelos* in Africa is *c.* 15 million years old (*C. minor* Morales & Pickford, 2008 from Kipsaraman; Morales & Pickford 2008), i.e. 9 million years older than *Bonisicyon*. There are three described species of African *Cynelos* (we are not at this point considering whether the African forms merit generic distinction as *Hecubides* Savage, 1965). Of these, two, *Cynelos macrodon* and *C. minor*, are only known from a few isolated teeth and will only be considered incidentally here. The third, *C. euryodon,* is better known and will form the main basis for comparison with *Bonisicyon* n. gen.

The m1 of *Bonisicyon* n. gen. resembles that of *C. euryodon* in several respects. However, most of these are shared primitive characteristics such as the proportions between trigonid and talonid, the relative size of paraconid and protoconid, the large, crest-like hypoconid and almost completely reduced entoconid, etc. They also differ in many respects, most prominent of which is the wholly reduced metaconid of *Bonisicyon* n. gen. The hypoconid is also much more strongly developed in the new taxon than in *C. euryodon*, as is the paraconid. In *Bonisicyon* n. gen. there is a distinct, sharp notch between protoconid and hypoconid, whereas in *C. euryodon* there is a much more gradual transition from protoconid to hypoconid. In *C. euryodon* the widest part of the m1 is level with the middle of the metaconid or slightly mesial to this point, in *Bonisicyon* n. gen. it lies further distally, possibly as a result of the reduction of the metaconid.

The m2 of *C. euryodon* is structurally very similar to that of *Bonisicyon* n. gen. though in the former the metaconid is less developed and the hypoconid more cusp-like. In addition, the m2 of *Bonisicyon* n. gen. is relatively shorter and wider, though the difference is slight (see below).

The M1 of *Bonisicyon* n. gen. is to all intents and purposes indistinguishable from that of *C. euryodon* except that its lingual end is somewhat wider and parallel-edged than in the latter taxon, in which the mesial and distal edges taper more gradually in a buccal to lingual direction.

METRIC COMPARISONS

To further circumscribe the morphology of *Bonisicyon* n. gen. relative to some other amphicyonids, Figure 3 shows a series of bivariate diagrams of dental proportions. Since we have established that *Bonisicyon* n. gen. is most comparable to *Cynelos* in size and shape, it is with this taxon that comparisons have been made.

Figure 3A shows the relationship between length and width of m1. In size, *Bonisicyon* n. gen. specimen HMD1/P11a matches a small *C. lemanensis*. The *Bonisicyon* n. gen. specimen has a broader m1 than the majority of other specimens, especially those of *C. euryodon*, and is only rivaled by some specimens of *C. lemanensis*. It may not be coincidental that the two *C. lemanensis* specimens with broad premolars are the two in the sample from the late Oligocene of Gaimersheim, Germany and the two oldest specimens referred to the species. These are only provisionally referred to *C. lemanensis*. It is also worth noting the considerable variation among the *C. euryodon* specimens, with specimen KNM-SO 1107 from Songhor (Schmidt-Kittler 1987: text-fig. 3a) being considerably smaller than the remaining m1 of the species.

Figure 3B shows the length of the m1 trigonid relative to the total length of the tooth. The diagram shows the trigonid of *Bonisicyon* n. gen. to be relatively short (i.e. the talonid is relatively long), but it is not outside the range of variation of European *Cynelos*, nor of *C. euryodon*. In the latter sample KNM-SO 1107 again stands out for its short m1 with short trigonid (long talonid).

Figure 3C shows the relationship between length and width of m2. The diagram shows the m2 of *Bonisicyon* n. gen. specimen ESC2/P224a to be about the size of a small *C. lemanensis* and somewhat wider than most *Cynelos*. However, the majority of specimens of *C. euryodon* also have relatively broad m2. This holds true for the three Rusinga specimens KNM-RU 4393 (Schmidt-Kittler 1987: text-fig. 2b, incorrectly given as RU 4394), KNM-RU 2956 (Schmidt-Kittler 1987: text-fig. 2c), and CMF 4027 (Savage 1965: fig. 52). These are also somewhat younger than the other illustrated *C. euryodon* and may indicate
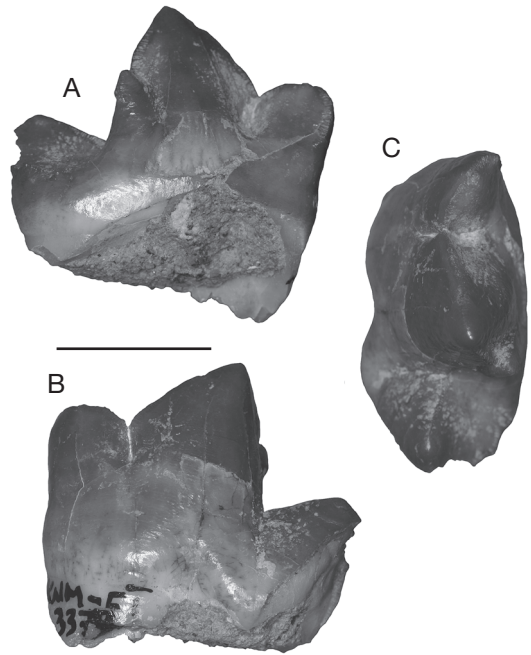

FIG. 2. — Left m1 KNM-FT 3379 of *Agnotherium* sp. from Fort Ternan, Kenya: **A**, lingual view; **B**, buccal view; **C**, occlusal view. Scale bar: 10 mm.

some morphological evolution within the lineage. At all events, the m2 of *Bonisicyon* n. gen. does not differ markedly in its proportions from m2 of *Cynelos* spp.

In Figure 3D, finally, are shown the relative length and width of M1. The *Bonicisyon* n. gen. M1 KNM-NK 45780 is of about the size of a medium *C. lemanensis*, i.e. relatively slightly larger than the m1 and m2 discussed above. It is also clearly mesiodistally longer and buccolingually shorter than *Cynelos* spp., with the exception of *C. euryodon*, some specimens of which are of similar proportions to *Bonisicyon* n. gen.

DISCUSSION

The most distinctive feature of *Bonisicyon illacabo* n. gen., n. sp. is, of course, the morphology of the holotype m1. Both m2 and M1 are broadly similar to other small- to medium-sized amphicyonids

such as *Cynelos* spp., but the m1 shows a number of autapomorphic features that clearly suggest generic-level distinction and make it difficult to pinpoint the exact phylogenetic relationships of this genus.

The tooth exhibits a curious mixture of features associated with increasing hypercarnivory and features that run counter to such an evolution. Among the former are the more equal size of paraconid and protoconid, the loss of the metaconid, the development of the hypoconid into a tall, shearing crest, the closing of the postvallid to form a notch of nearly the same morphology as the carnassial notch between paraconid and protoconid, and the strictly mesiodistal carnassial shear that incorporates the hypoconid. Yet these features are not accompanied by other features generally associated with hypercarnivory, such as a narrower tooth, taller trigonid cuspids and shortened talonid. The trigonid cuspids are quite blunt, especially compared with other relatively hypercarnivorous amphicyonids, such as Fort Ternan *Agnotherium* (Fig. 2) and *Magericyon* from Batallones-1 in Spain (Peigné *et al.* 2008). The tooth (and m2) is broad compared to otherwise similar amphicyonids (Fig. 3A, C), and the talonid is relatively long (Fig. 3B), much longer than in, e.g., *Agnotherium* and *Magericyon*.

Finally, it may be noted that although the data are poor at best, there are some features of *Bonisicyon* n. gen., such as the broad lower molars and well-developed M1 protocone, that may, together with the lack of evidence of a *Bonisicyon*-like form outside Africa or of a migration of Amphicyonidae into Africa after the early middle Miocene, argue for a derivation of the genus from early Miocene African amphicyonids such as *C. euryodon*. If this is the case, there may be merit in resurrecting *Hecubides* for these forms, as suggested on other grounds by Morales *et al.* (2007). However, this line of evidence will not be truly useful until intermediate forms are recovered from the African late early and middle Miocene. Given the present evidence, *Bonisicyon illacabo* n. gen., n. sp. stands distinctly apart from other Amphicyonidae in Africa as well as in the late Miocene globally.

DATING, ENVIRONMENT, AND THE EXTINCTION OF AMPHICYONIDAE

All of the fossils of *Bonisicyon illacabo* n. gen., n. sp. discussed above are Messinian in age. The Lothagam specimen is from the Upper Nawata Formation, dated *c.* 6.5-5.0 Ma, with the base better dated than the top (McDougall & Feibel 1999). By comparison with other faunas of similar age, it seems to us unlikely that the upper Nawata Formation includes Pliocene elements, so the top of this time slice is here taken as 5.3 Ma. The Lemudong'o specimen is dated *c.* 6.1-6 Ma (Ambrose *et al.* 2007b). Of the Gona specimens, those from ABD and HMD are dated 6.4-6.2 Ma, while the ESC specimen is dated 6.0-5.5 Ma (Kleinsasser *et al.* 2008; Quade *et al.* 2008). Thus, the time span of the species judged from the available fossils is constrained to a time slice of about 0.5 Ma either side of 6 Ma. The youngest specimens are the Lothagam mandibular ramus and the ESC m2 from Gona. These latest Miocene specimens are likely to represent the youngest known amphicyonid specimens, unless the Siwalik material mentioned above can be shown to be younger, which at present appears unlikely. If this is correct, the last amphicyonid, at least in Africa, became extinct at the very end of the Miocene, and in its small size and derived dental characters is quite different from the last amphicyonids from Europe and Asia, which were very large omnivores (see review above). Although the available material leaves little room for certainty, we would like to conclude by presenting a scenario for why this last amphicyonid had these attributes and why it became extinct.

The mid-Vallesian crisis (see, e.g., Fortelius *et al.* 1996) was a time of major environmental change that led to a substantial turnover of mammals in western Europe. The environmental change, characterized by an extension of open habitats and retraction of forests, led to a decrease in the diversity of browsers and of carnivores tied to closed habitats. Among the latter were the Amphicyonidae, the last of which were very large forms of mainly omnivirous dental aspect. They are all but gone from western Eurasia by MN 11 (Viranta 1996). The same story holds true in its essentials for the Indian subcontinent and Africa. In the latter continent, with the exception of *Bonisicyon* n. gen., all the late Miocene amphi-
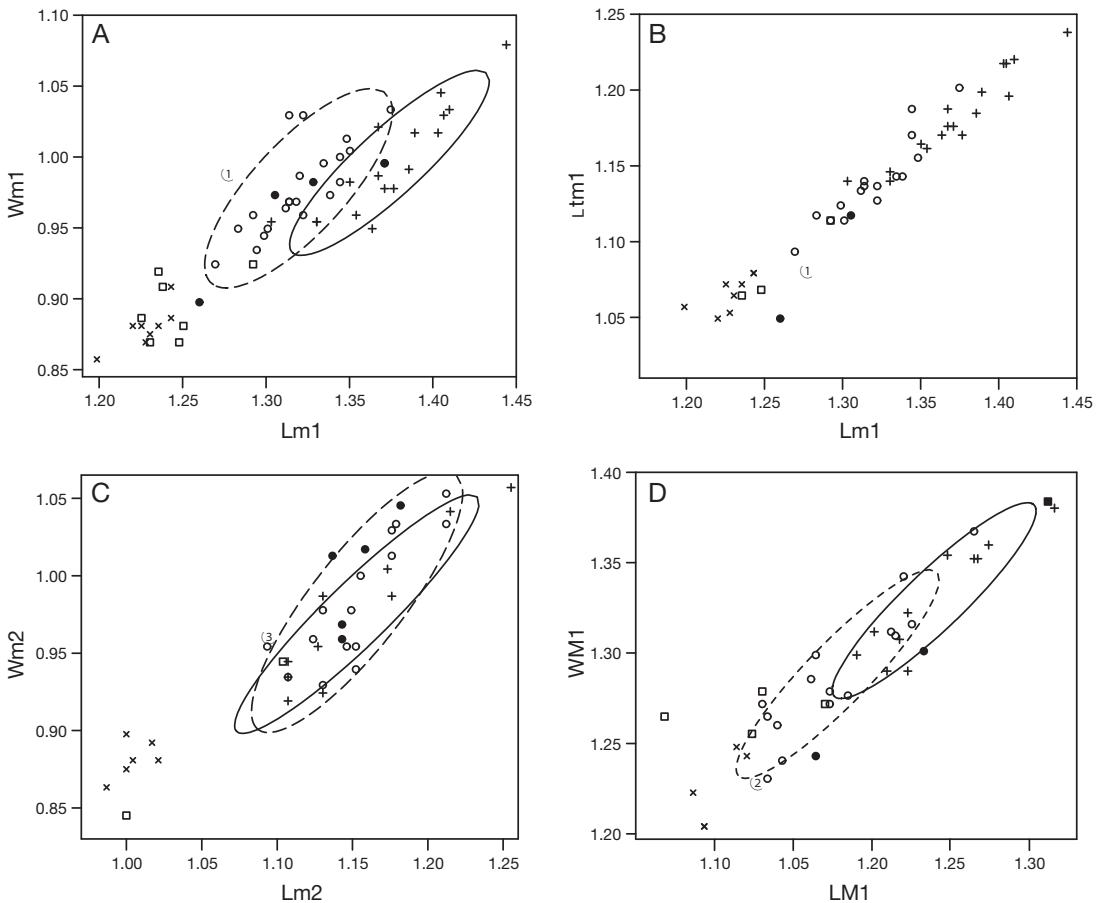
FIG. 3. — Bivariate diagrams comparing the metrics of *Bonisicyon illacabo* n. gen., n. sp. with those of African *Cynelos* Jourdan, 1862 and selected species of European *Cynelos* of comparable size. The ellipses are 95% confidence ellipses of *C. helbingi* (Dehm, 1950) (solid line) and *C. lemanensis* (Pomel, 1846) (dashed line): **A**, length versus width of m1; note the relatively great width of the m1 of *Bonisicyon* n. gen.; **B**, total length of m1 versus trigonid length; the correlation is high here and the confidence ellipses were omitted as they obscure the symbols; the trigonid of the m1 of *Bonicisyon* is relatively short; **C**, length versus width of m2. Note by comparison with A that the m2 of *C. helbingi* is relatively short compared to that of *Bonisicyon* n. gen., African *Cynelos*, and *C. lemanensis.* Note also that the width of the m2 of *Bonisicyon* n. gen., like that of the m1, is relatively great; **D**, length versus width of M1. Note that here, as in A-C, the size of the *Bonisicyon* n. gen. tooth is close to that of a small *C. lemanensis* and also that, like African *Cynelos*, it is relatively buccolingually short. Symbols: **1**, HMD1/P11a; **2**, Lemundong'o KNM-NK 45780; **3**, Gona ESC2/P224a; ●, *C. euryodon* (Savage, 1965); ○, *C. lemanensis*; □, *C. rugosidens* (Schlosser, 1899); ■, *C. macrodon* (Schlosser, 1899); **+***, C. helbingi*; ✕, *C. schlosseri* (Dehm, 1950).

cyonids, including *Myacyon dojambir* and unnamed amphicyonids from Samburu Hills, Lothagam, and Toros-Menalla (cf. Werdelin & Peigné in press) are very large forms.

The exception to the pattern is *Bonisicyon* n. gen. From the available remains, we can state that it is a small form (for an amphicyonid) and trending distinctly to hypercarnivory. The environmental context

of the *Bonisicyon* n. gen. specimens is poorly known, as is generally true of East African late Miocene localities. The Upper Nawata may best be characterized as a mixed environment, though trending towards open habitat (Leakey *et al.* 1996). There are two fossiliferous layers at Lemudong'o that suggest a transition from more closed to more open habitat (Ambrose *et al.* 2007a). Unfortunately, the exact

provenance of the KNM-NK 45780 specimen is not known. Only from Gona do we have a more consistent environmental signal. Recent isotope studies there (Levin *et al.* 2008) suggest that the environment at the HSD and AMD sites was bushland to grassland, rather than forest. This may suggest a habitat shift in this last amphicyonid, or at least that it was adapted to a different habitat spectrum than the large-sized forms that preceded it. This adaptation to a new dominant habitat type may have been successful, but at about the same time, the first medium-sized canids (jackal- to coyote-sized species of *Eucyon* Tedford & Qiu, 1996) reached Africa (e.g., Morales *et al.* 2005). By then, the Canidae Fischer, 1817 family had a long history of adaptation to open habitats (Andersson & Werdelin 2003) and we suggest that this new competitor was the death-knell for the last amphicyonid, despite the late attempt to adapt to changing circumstances.

This scenario is clearly speculative and needs to be validated in a number of ways, of which two are the most obvious. First and foremost, more finds of late Miocene African amphicyonids are needed, especially of the postcrania, to see if the adaptational story holds up. Second, habitat differences between localities with and without *Bonisicyon* n. gen. or related forms should be studied (though it must be kept in mind that these forms are rare and absence of evidence isn't necessarily evidence of absence). Nevertheless, the possibility that the last amphicyonid may have been successful in adapting to the changing environment if not for immigration of a competitor is intriguing.

REFERENCES

AMBROSE S. H., BELL C. J., BERNOR R. L., BOISSERIE J.-R., DARWENT C. M., DEGUSTA D., DEINO A., GARCÍA N., HAILE-SELASSIE Y., HEAD J. J., HOWELL F. C., KYULE M. D., MANTHI F. K., MATHU E. M., NYAMAI C. M., SAEGUSA H., STIDHAM T. A., WILLIAMS M. A. J. & HLUSKO L. J. 2007a. — The paleoecology and paleogeographic context of Lemudong'o Locality 1, a late Miocene terrestrial fossil site in southern Kenya. *Kirtlandia* 56: 38-52.

AMBROSE S. H., NYAMAI C. M., MATHU E. M. & WILLIAMS M. A. J. 2007b. — Geology, geochemistry, and stratigraphy of the Lemudong'o Formation, Kenya Rift Valley. *Kirtlandia* 56: 53-64.

ANDERSSON K. & WERDELIN L. 2003. — The evolution of cursorial carnivores in the Tertiary: implications of elbow joint morphology. *Proceedings of the Royal Society Biological Sciences (supplement)* 270: S163-S165.

BARRY J. C., LINDSAY E. H. & JACOBS L. L. 1982. — A biostratigraphic zonation of the middle and upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology* 37: 95-130.

FORTELIUS M., WERDELIN L., ANDREWS P., BERNOR R. L., GENTRY A., HUMPHREY L., MITTMANN H.-W. & VIRANTA S. 1996. — Provinciality, diversity, turnover, and paleoecology in land mammal faunas of the later Miocene of western Eurasia, *in* BERNOR R. L., FAHLBUSCH V. & MITTMANN H.-W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York: 414-448.

GINSBURG L. 1977. — Les carnivores du Miocène de Beni Mellal (Maroc). *Géologie méditerranéenne* 4: 225-240.

HOOIJER D. A. 1963. — Miocene Mammalia of Congo. *Annales, Musée royal de l'Afrique Centrale*, Sér. in 8°, 46: 1-77.

HOWELL F. C. & GARCÍA N. 2007. — Carnivora (Mammalia) from Lemudong'o (late Miocene: Narok District, Kenya). *Kirtlandia* 56: 121-139.

HUNT R. M. JR 2002. — Intercontinental migration of Neogene amphicyonids (Mammalia, Carnivora): appearance of the Eurasian beardog *Ysengrinia* in North America. *American Museum Novitates* 3384: 1-53.

KLEINSASSER L., QUADE J., LEVIN N. E., SIMPSON S. W.,

McIntosh W. & Semaw S. 2008. — Geochronology of the Adu-Asa Formation at Gona, Ethiopia, *in* Quade J. & Wynn J. G. (eds), The geology of early humans in the Horn of Africa. *The Geological Society of America Special Paper* 446: 33-65.

Kurtén B. 1976. — Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia. *Notes du Service géologique de Tunisie* 42: 177-214.

Leakey M. G., Feibel C. S., Bernor R. L., Harris J. M., Cerling T. E., Stewart K. M., Storrs G. W., Walker A., Werdelin L. & Winkler A. J. 1996. — Lothagam: a record of faunal change in the late Miocene of East Africa. *Journal of Vertebrate Paleontology* 16: 556-570.

Levin N. E., Simpson S. W., Quade J., Cerling T. E. & Frost S. R. 2008. — Herbivore enamel carbon isotopic composition and the environmental context of *Ardipithecus* at Gona, Ethiopia. *in* Quade J. & Wynn J. G. (eds), The geology of early humans in the Horn of Africa. *The Geological Society of America Special Paper* 446: 215-234.

McDougall I. & Feibel C. S. 1999. — Numerical age control for the Miocene-Pliocene succession at Lothagam, a hominoid-bearing sequence in the northern Kenya Rift. *Journal of the Geological Society, London* 156: 731-745.

Morales J. & Pickford M. 2005. — Carnivores from the middle Miocene Ngorora Formation (13-12 Ma), Kenya. *Estudios Geológicos* 61: 271-284.

Morales J. & Pickford M. 2008. — Creodonts and carnivores from the middle Miocene Muruyur Formation at Kipsaraman and Cheparawa, Baringo District, Kenya. *Comptes rendus Palevol* 7: 487-497.

Morales J., Pickford M., Soria D. & Fraile S. 1998. — New carnivores from the basal middle Miocene of Arrisdrift, Namibia. *Eclogae Geologicae Helvetiae* 91: 27-40.

Morales, J., Pickford, M. & Soria, D. 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., Pickford M. & Soria D. 2007. — New carnivoran material (Creodonta, Carnivora and *incertae sedis*) from the early Miocene of Napak, Uganda. *Paleontological Research* 11: 71-84.

Morales J., Pickford M. & Salesa M. J. 2008. — Creodonta and Carnivora from the early Miocene of the northern Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia* 20: 291-310.

Morlo M., Miller E. R. & El-Barkooky A. N. 2007. — Creodonta and Carnivora from Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology* 27: 145-159.

Peigné S., Chaimanee Y., Yamee C., Tian P. & Jaeger J.-J. 2006. — A new amphicyonid (Mammalia, Carnivora, Amphicyonidae) from the late middle Miocene of northern Thailand and a review of the amphicyonid record in Asia. *Journal of Asian Earth Sciences* 26: 519-532.

Peigné S., Salesa M. J., Antón M. & Morales J. 2008. — A new amphicyonine (Carnivora: Amphicyonidae) from the upper Miocene of Batallones-1, Madrid, Spain. *Palaeontology* 51: 943-965.

Pickford M., Senut B., Gommery D. & Musiime E. 2003. — New Catarrhine fossils from Moroto II, early middle Miocene (*c.* 17.5 Ma) Uganda. *Comptes rendus Palevol* 2: 649-662.

Pilgrim G. E. 1932. — The fossil Carnivora of India. *Memoir of the Geological Survey of India. Paleontologica Indica* 18: 1-232.

Quade J., Levin N. E., Simpson S. W., Butler R., McIntosh W., Semaw S., Kleinsasser L., Dupont-Nivet G., Renne P. & Dunbar N. 2008. — The geology of Gona, Afar, Ethiopia. *in* Quade J. & Wynn J. G. (eds), The geology of early humans in the Horn of Africa. *The Geological Society of America Special Paper* 446: 1-31.

Savage R. J. G. 1965. — Fossil mammals of Africa: 19. The Miocene Carnivora of East Africa. *Bulletin of the British Museum (Natural History), Geology* 10: 241-316.

Schmidt-Kittler N. 1987. — The Carnivora (Fissipedia) from the lower Miocene of East Africa. *Palaeontographica*, Abt. A 197: 85-126.

Sudre J. & Hartenberger J.-L. 1992. — Oued Mya 1, nouveau gisement de mammifères du Miocène supérieur dans le sud Algérien. *Geobios* 25: 553-565.

Tsujikawa H. 2005. — The updated late Miocene large mammal fauna from Samburu Hills, northern Kenya. *African Study Monographs* Supplementary issue 32: 1-50.

Viranta S. 1996. — European Miocene Amphicyonidae – taxonomy, systematics and ecology. *Acta Zoologica Fennica* 204: 1-61.

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.

Werdelin L. 2003. — Mio-Pliocene Carnivora from Lothagam, Kenya, *in* Leakey M. G. & Harris J. D. (eds), *Lothagam: Dawn of Humanity in Eastern Africa*. Columbia University Press, New York: 261-328.

Werdelin L. 2005. — The Carnivora of Rudabánya (MN 9, late Miocene, Hungary), *in* Bernor R. L., Kordos L. & Rook L. (eds), Multidisciplinary research at Rudabánya. *Palaeontographia Italica* 90: 163-180.

Werdelin L. & Peigné S. in press. — Carnivora, *in* Werdelin L. & Sanders W. J. (eds), *Cenozoic Mammals of Africa*. University of California Press, Berkeley.