

Systematics of African Amphicyonidae, with descriptions of new material from Napak (Uganda) and Grillental (Namibia)

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Abstract

The Early Miocene Napak XV locality (ca 20.5 Ma), Uganda, has yielded an interesting assemblage of fossils, including the very well represented amphicyonid *Hecubides euryodon*. The remarkable find of a nearly complete mandible, unfortunately with poorly preserved dentition, together with new dental remains allow us to obtain a better idea about the morphology and variability of this species. Additionally, we describe a newly discovered mandible of *Hecubides euryodon* from the Grillental-VI locality (Sperrgebiet, Namibia), which is the most complete and diagnostic Amphicyonidae material found in this area. Comparisons with *Cynelos lemanensis* from Saint-Gérand-le-Puy (France), the type locality, and with an updated sample of the species of amphicyonids described in Africa leads us to validate the genus *Hecubides*. *Hecubides* would be phylogenetically related to the medium and large size species of Amphicyonidae from Africa, most of them now grouped into the genera *Afrocyon* and *Myacyon*, both endemic to this continent.

Keywords: Carnivora, Amphicyonidae, Miocene, Africa, Systematics

Resumen

La localidad del Mioceno inferior de Napak XV (ca 20,5 Ma) ha suministrado un interesante conjunto de fósiles, entre los que el anfícionido *Hecubides euryodon* está bien representado. Es importante el hallazgo de una mandíbula bastante completa, aunque con dentición bastante deteriorada y nuevos materiales dentarios que nos permiten un mejor conocimiento de la morfología y variabilidad de esta especie. Adicionalmente, se describe una nueva mandíbula, también de *Hecubides euryodon*, procedente del yacimiento de Grillental-VI (Sperrgebiet, Namibia), que viene a ser el material más completo y diagnóstico de esta especie en este área. Comparaciones con *Cynelos lemanensis* de Saint-Gérand-le-Puy (Francia), localidad tipo de esta especie, y con los amphicyonidos descritos hasta el presente en África, nos conducen a validar el género *Hecubides*. Este género estaría relacionado filogenéticamente con las especies de talla media y grande de Amphicyonidae de África, la mayoría de ellas ahora agrupadas en los géneros *Afrocyon* y *Myacyon*, ambos endémicos de este continente.

Palabras clave: Carnivora, Amphicyonidae, Mioceno, África, Sistemática

1. Introduction

On the slopes of Akisim, Napak, Uganda (Fig. 1), extensive tree-cutting for the manufacture of charcoal has led to soil erosion in some sectors of the mountain, thereby exposing the underlying volcano-sedimentary deposits, which have long been known to yield abundant fossils (Musalizi *et al.*, 2009).

One such erosion feature found in 2007 is the richly fossiliferous locality of Napak XV, not far from Napak V. Excavated over the next few years Napak XV yielded an astonishing variety of well preserved fossils including a complete skull of a gymnophionan (Rage and Pickford, 2011), articulated skeletons of rodents (Pickford *et al.*, 2013, 2014), a skull and some postcranial remains of *Ugandapithecus* (Musalizi *et al.*,

2009), a diversity of small apes (Pickford *et al.*, 2010), and an assorted array of amphicyonid remains, which form the basis for the present revision.

Information about the geology of the volcanic setting of Napak is to be found in papers by King (1949), Trendall (1965), and Bishop and Trendall (1967), and other publications of a broad nature (Bishop *et al.*, 1969; Pickford, 1986a; 1986b; 1986c). General works on the fauna, taphonomy and faunas are available (Bishop, 1958a; 1958b; 1962; 1963a; 1963b; 1964a; 1964b; 1967; 1968; 1971; 1972; Bishop and Trendall, 1967; Bishop and Whyte, 1962; Musalizi *et al.*, 2009; Pickford and Senut, 1988; Pickford *et al.*, 1986; Trickler *et al.*, 1963).

Specialist studies of the fauna (Table 1) have been published. Pickford (1995, 2004) studied the fossil land snails from Napak. Rage and Pickford (2011) described a complete skull of a gymnophionan. Primates were dealt with by Allbrook and Bishop (1963) and other researchers (Bishop, 1964a; Fleagle, 1975; Fleagle and Simons, 1978; Gommery *et al.*, 1998, 1999, 2002; Harrison, 1982, 1988; Leakey, 1967; Pickford *et al.*, 2010; Pilbeam, 1969; Pilbeam and Walker,

1968; Rafferty *et al.*, 1995; Senut *et al.*, 2000; Simpson, 1967; Walker, 1969, 1974, 1978). Butler (1962, 1978a, 1978b, 1984) described the chalicotheres and insectivorans from the deposits. Hooijer (1966) and Guérin and Pickford (2003) dealt with the rhinocerotids from Napak, while Lavocat (1973) and Pickford *et al.* (2013, 2014) described the rodents. Morales *et al.* (2001, 2007) described new carnivorans from Napak following up on the pioneer work by Savage (1965) and the later studies by Schmidt-Kittler (1987) and Schmidt-Kittler and Heizmann (1991). The ruminants were studied by Pickford (2002) and Sánchez *et al.* (2015). Hyracoids were published by Tsujikawa and Pickford (2006) and Pickford (2013). Suids were studied by Wilkinson (1976) and Pickford (1986d).

The Napak deposits comprise predominantly sub-aerial volcanic ashes of carbonaticitic and nephelinitic composition and palaeosols derived from these ashes. The base of the succession, called the Iriri Member, contains palaeosols and fluvio-palustral sediments, some of which are extremely rich in fossil remains. The higher levels of the succession, comprising the Napak Member, in which the sites of Napak I, IV, V, IX and XV occur, show few if any signs of aquatic

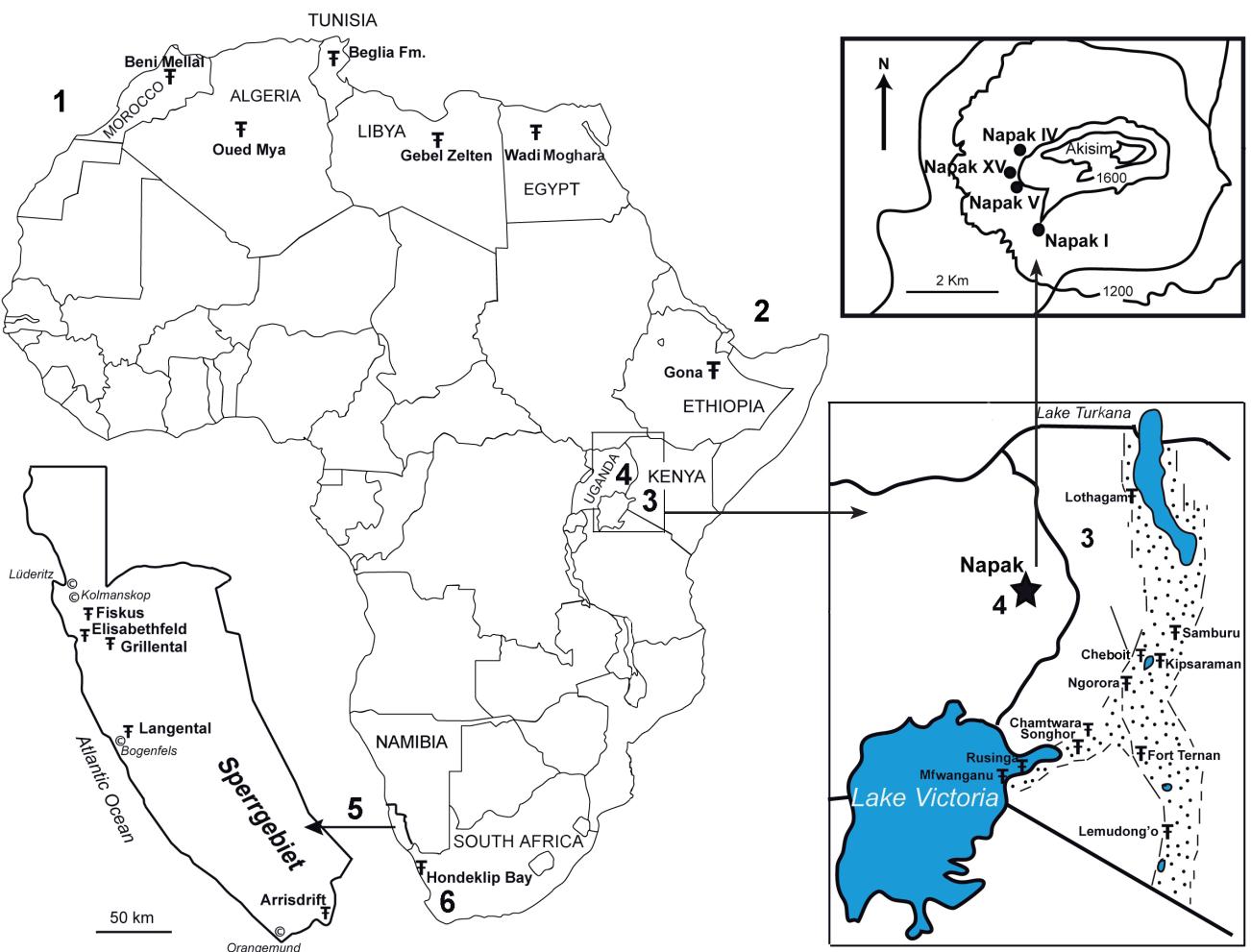


Fig. 1.- Geographic location of African Miocene localities that have yielded Amphicyonidae remains. 1.- North Africa. 2.- Ethiopia. 3.- Kenya. 4.- Uganda, showing the location of the fossiliferous deposits of Napak in the north-east of the country, close to the western edge of the Gregory Rift Valley. 5.- Namibia, showing the location of fossil localities in Sperrgebiet. 6.- South Africa.

GASTROPODA	AVES	Rodentia	Primates	Incertae sedis
<i>Maizanita lugubrioides</i>	Large sp.	<i>Diamantomys fuederitzii</i>	<i>Mioeuoticus bishopi</i>	<i>Prionogale breviceps</i>
<i>Maizaniella</i> sp.	Hornbill	<i>Paraphiomys pigotti</i>	<i>Progalago dorae</i>	<i>Kelba quadeemae</i>
<i>Tholachatina leakeyi</i>	Medium sp.	<i>Paraphiomys stromeri</i>	<i>Komba robustus</i>	Carnivora
<i>Burtoa nilotica</i>	Small sp.	<i>Epiphiomys coryndoni</i>	<i>Komba minor</i>	<i>Heubibides euryodon</i>
<i>Subulona</i> sp.	REPTILIA			
<i>Oreohomorus</i> sp.	Ophidea	<i>Miophiomys arambourgi</i>	<i>Prohylobates</i> sp.	? <i>Kichechia zamanae</i>
<i>Opeas</i> sp.	Gymnophione	<i>Megapedetes pentadactylus</i>	<i>Micropithecus clarki</i>	<i>Ugandictis napakensis</i>
<i>Edouardia</i> sp.	Lacertidae	<i>Reneffosor songhorensis</i>	<i>Limnopithecus legetet</i>	<i>Ginsburgsmilus napakensis</i>
<i>Conulinus</i> sp.	Chamaeleonidae	<i>Proheliophobius</i> sp.	<i>Kalepithecius songhorensis</i>	Perissodactyla
<i>Krapfiella</i> sp.	Varanidae	<i>Vulcanisciurus africanus</i>	<i>Lomorupithecius evansi</i>	<i>Butleria rusingense</i>
<i>Koruella magnifica</i>	Chelonii	<i>Nonanomalurus soniae</i>	<i>Iriripithecius alekileki</i>	<i>Aceratherium</i> sp.
<i>Thapsia</i> sp.	Crocoyliidae	<i>Paranomalurus bishopi</i>	<i>Karamojapithecius akismia</i>	<i>Brachypotherium</i> sp.
<i>Trochonanina</i> sp.	<i>Brochuchus pigotti</i>	<i>Paranomalurus walkeri</i>	<i>Dendropithecus ugandensis</i>	<i>Ougandatherium napakensis</i>
<i>Trochozonites</i> sp.	MAMMALIA			
<i>Pupoidea</i> sp.	Insectivora	<i>Afrocrecideton songhorensis</i>	<i>Turkanapithecus rusingensis</i>	Artiodactyla
<i>Ptychotrema</i> sp.	<i>Amphechinus rusingensis</i>	<i>Gomphotheriidae</i>	? <i>Proconsul nyanzae</i>	<i>Brachyodus aequatorialis</i>
? <i>Macrogonaxis</i> sp.	<i>Protenrec tricuspid</i>	<i>Progomphotherium cf maraisi</i>	<i>Ugandapithecus major</i>	<i>Nguruwe kijivium</i>
<i>Gulella</i> sp. 1	<i>Erythrozootes chamerpes</i>	<i>Archaeobelodon</i> sp.	Creodontia	
<i>Gulella</i> sp. 2	Macroscelidae	<i>Deinotheriidae</i>	<i>Metasinopa napaki</i>	<i>Diamantohyus africanus</i>
<i>Tayloria</i> sp.	<i>Myohyrax</i> sp.	<i>Deinotherium hobleyi</i>	<i>Pterodon africanus</i>	<i>Afrotragulus parvus</i>
<i>Haplonepiion naggisi</i>	<i>Miorhynchocyon</i> sp.	<i>Orycteropodidae</i>	<i>Isohyaenodon piligrimi</i>	<i>Siamotragulus songhorensis</i>
<i>Edentulina rusingensis</i>	Chiroptera	<i>Orycteropus africanus</i>	<i>Isohyaenodon zadoki</i>	<i>Dorcatherium iririensis</i>
INSECTA		<i>Hyracoidea</i>	<i>Leakitherium hiwegi</i>	<i>Walangania africanus</i>
Millipedes	Indet sp.	<i>Brachyhyrax aequatorialis</i>	<i>Teratodon spekei</i>	
Moth cocoons		<i>Meroehyrax bateae</i>		
Termite bioconstructions				

Table 1.- Updated Faunal List from Napak, Early Miocene (Uganda).

deposition, being, in large measure, composed of subaerially deposited volcanic ash and immature palaeosols.

Seeds of *Celtis* are common in Napak XV, as are fragmentary leaves of dicotyledons, and stems of grasses or sedges and plant root traces. Fossil tree trunks are quite common in the agglomerates overlying the Napak Member, some layers of which contain abundant plant remains (wood, fruit, and leaves).

Fossils vertebrates in the Napak Member tend to occur as isolated fragments, but Napak XV is unusual in this respect, having yielded partial skeletons of a variety of vertebrates (crocodiles, rodents) and almost complete cranial remains (gymnophionan, *Ugandapithecus*, rodents, insectivores) and dentognathic fossils (relatively complete maxillae and mandibles of *Limnopithecus*, amphicyonids, tragulids, pecorans, suids).

The Napak deposits accumulated ca 20.5 Ma (Sawada *et al.*, in progress) which correlates with the early Miocene (Aquitanian-Burdigalian of Europe). The palaeoenvironment on the slopes of the volcano was evidently forested with some open patches as shown by the fossil land snails (Pickford, 2004), and the domination of brachyodont and bunodont dentitions among the mammals. Open grassy areas did exist in the vicinity, as attested by the presence of hypsodont rodents (*Diamantomys*) (Lavocat, 1973), macrosCELIDIDS (*Myohyrax*) (Butler, 1962, 1978a) and rhinocerotids (*Ougandatherium*) (Guérin and Pickford, 2003).

This paper deals with the Napak amphicyonids *Hecubides euryodon* and *Afrocyon* sp. which are the largest fissiped carnivores known from the site, although they would have

been dwarfed by the creodont *Pterodon africanus*. *Hecubides euryodon* and the slightly smaller barbourofelid *Ginsburgsmilus napakensis* would have had ample prey species at their disposal, concomitant with their body dimensions, including primates, hyracoids, suids and several ruminants (Table 1). Many of the fossil bones at Napak show bite marks and gnawing marks due to carnivore activity, as well as parallel gnawing traces made by rodents.

A note on an amphicyonid mandible from the Early Miocene of Grillental-VI, Sperrgebiet, Namibia (Fig. 1) attributed to *Hecubides euryodon*, is included in order to contribute to the knowledge of this important species. Grillental-VI is located in the fossiliferous valley-fill sediments of the Northern Sperrgebiet, which are faunally similar to East African sites such as Songhor, Koru and Napak and to other Sperrgebiet sites such as Langental, Elisabethfeld and Grillental I-IV, that are attributed to the Early Miocene, dated about 21-19 Ma (Pickford and Senut, 2008). The paper ends with a general discussion about African amphicyonids, including late Miocene forms.

The new material from Napak (NAP) described here is stored in the Uganda Museum (Kampala, Uganda). Fossils from the Speergebiet localities Arrisdrift (AD), Grillental (GT), Fiskus (FK) are curated in the Museum of the Geological Survey of Namibia (Windhöek, Namibia). Other specimens from Napak (NHM), Rusinga (NHM) and Gebel Zelten (NHM) are preserved in the Natural History Museum (London, UK). Specimens from *Cynelos lemanensis* from Saint-Gérand-le-Puy (SG) are curated in the Muséum Nationale d'Histoire Naturelle (Paris, France).

2. *Hecubides* Systematic Description

ORDER Carnivora Bowdich, 1821

FAMILY Amphicyonidae Haeckel, 1866

SUBFAMILY Amphicyoninae Haeckel, 1866

GENUS *Hecubides* Savage, 1965

Included species: *Hecubides euryodon* Savage, 1965 (type species) and *Hecubides minor* Morales and Pickford, 2008.

Hecubides euryodon Savage, 1965

Type Locality: Napak I.

Age: Early Miocene (Faunal Set I, ca 20.5 Ma).

Holotype: NHM M-19805 (London), maxilla containing P3-P4, M1-M2, and alveoli of P2 and M3 on both sides (Savage, 1965, Pl. 5-1).

Other localities: Uganda (Napak IV, Napak V, Napak XV); Kenya (Chamtwara, Koru, Mfwanganu, Rusinga, Songhor); Namibia (Grillental VI, Langental, Elisabethfeld).

Original Diagnosis: in Savage (1965, p. 289).

Emended Diagnosis: Amphicyoninae of medium size, similar in dimensions to European *Cynelos lemanensis* (Saint-Gérand-le-Puy, France). M3 and m3 not reduced, M1 and M2 similar to each other in size. M1 subtriangular, with well-developed metaconule united to the protocone, lingual part with a tendency to reduction. M2 subquadrate with broad lingual part. P4 with distinct protocone, and an incipient to well-developed parastyle. Mandible much elongated with diastemata between the premolars. The p4 has a strongly developed posterior cuspid, m1 with strong and voluminous metaconid, m2 big with reduced to absent paraconid, narrow talonid almost completely occupied by the hypoconid.

2.1. New material from Napak XV

NAP XV 97'07+150'07+91'08 right mandible comprised of three fragments found during different field seasons (Fig. 2-1). NAP XV 15'00, left mandible fragment, including part of the ascending ramus with the articular condyle. NAP XV 96'09, two fragments of left mandible, with part of the horizontal ramus, containing poorly preserved teeth. The state of preservation and wear of the teeth indicate that all these fragments, which were found close together, could comprise a single individual. NAP XV 162'08, moderately worn right m2 (Fig. 2-5); NAP XV 4'12, right m1; NAP XV 382'08, right M1 (Fig. 2-3); NAP XV 98'07, right M1 (Fig. 2-4); NAP XV 180'08, left M1 with damaged paracone-metacone; NAP XV 146'08, heavily worn left M2; NAP XV 127'07, deeply worn right M2; NAP XV 76'08, P4 (Fig. 2-2); NAP IX 14'02, right calcaneum (Fig. 3). Measurements in Table 2.

Description

Mandible. NAP XV 97'07+150'07+91'08. The mandible is noticeably elongated (Fig. 2-1), very similar in dimensions

Locality	Species	Specimen	Tooth	Length	Width
Napak XV	<i>Hecubides euryodon</i>	NAP XV-76'08	P4	18.3	10.1
		NAP XV-98'07	M1	14.8	18.5
		NAP XV-382'08	M1	15.4	19.9
		NAP XV-180'08	M1	—	—
		NAP XV-146'08	M2	11.5	15.5
		NAP XV-127'07	M2	11.6	15.5
			p4	11	4.9 *
		NAP XV-150'07	m1	20*	9
			m2	14*	7*
			m3	8*	5.5
Grillental VI	GT 35'15	NAP XV- 96'07	p4	12.1	5.7
			m2	12.8*	7.5
		NAP XV 4'12	m1	21.1	10.2
			p3	11.3**	—
			p4	12.4	6.5
Napak I	<i>Afrocyon</i> sp.	GT 35'15	m1	18.7	8.6
		NAP-I 7'99	m2	12.8	8.3
Rusinga	<i>Afrocyon macrodon</i>	NHM M-19086	m3	6.9**	4**
		NHM M-34303	m1	25.8	11.6

Table 2.- Upper and lower teeth measurements (in mm) of *Hecubides euryodon* from Napak XV (Uganda) and Grillental VI (Namibia). *Afrocyon* sp. from Napak I (Uganda). *Afrocyon macrodon* from Rusinga (Kenya). * (c.a.) and ** (alveolus).

and proportions to that of *Cynelos lemanensis* from Saint-Gérand-le-Puy (SG-490) figured by Ginsburg (1977). The dental series is damaged, only the canine, p3 and p4 being complete, although the last tooth is deeply worn, as is the canine. The p2 presents a small crack, and only the base of the m1 is preserved. The m3, m2 and p1 are missing, their alveoli filled with sediment. There are gaps between all the premolars and there is even a short diastema between the p4 and the m1 and a longer one between the canine and the p1. The p3, which is well preserved, is a small tooth with a low, elongated crown, with a main cusp showing long anterior and posterior crests. Posteriorly there is a small swelling, which interrupts the slope, forming a tiny, barely visible, cusplet. The p4 is also elongated but the crown is broken. The p2 was very reduced and, on the basis of its alveolus, the p1, which is missing, was uniradiculate. The jaw is broken distally in the region of the condyle. However, NAP XV 15'00, a left mandible fragment preserves the condyle in excellent condition, showing that it was short and lingually very broad. NAP XV 96'09, a fragment of left mandible, is heavily deformed (probably trampled) preserving the complete but deeply worn m2 and a damaged p4. NAP XV 162'08, a right m2 is quite worn lingually, missing the apex of the metaconid, but preserving a strong, globose protoconid (Fig. 2-5). The paraconid was probably absent, although the state of preservation of the tooth does not permit a firm conclusion to be reached, although close inspection reveals that the trigonid valley was very small, tall and closed anteriorly. The talonid is narrow, short, and has also lost its enamel, although it is possible to see that there is a swelling for the hypoconid, which would have occupied a large part of the surface of the talonid. NAP XV 4'12, is a well preserved right m1 with minor occlusal wear which affects the buccal wall and the apex of the proto-

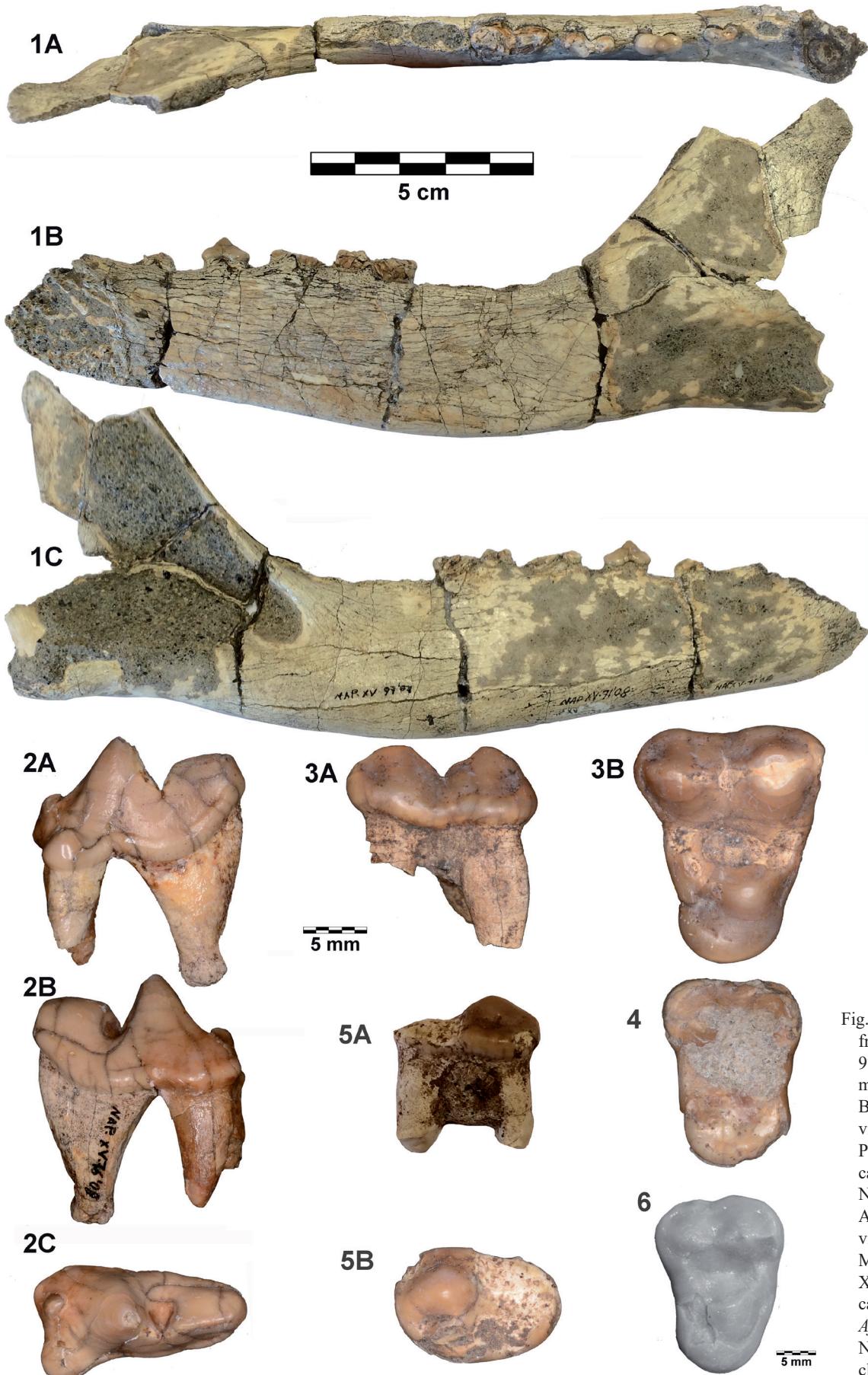


Fig. 2.- *Hecubides euryodon* from Napak-I. 1. NAP XV 97°07'+150°07'+91°08'. A) occlusal view. B) lingual view. C) buccal view. 2. NAP XV 76°08', left P4. A) lingual view. B) buccal view. C) occlusal view. 3. NAP XV 382°08', right M1. A) buccal view. B) occlusal view. 4. NAP XV 146°08', left M2, occlusal view. 5. NAP XV 162°08', right m2. A) buccal view. B) occlusal view. 6. *Afrocyon* sp. from Napak-I, NAP I 7°99', right M2 in occlusal view.

conid and to a lesser extent, the anterior part of the paraconid and hypoconid. Lingually, the wear is heavier extending from the apex of the paraconid to the protoconid-metacanid and the hypoconid. The molar is gracile, with a relatively long paraconid, with an almost vertical anterior cristid and the metacanid is voluminous. The talonid is long, and broad, and is almost completely occupied by a globose, relatively low, hypoconid, which joins a peripherally positioned entocristid which extends to the base of the metacanid. The cingula are weak, almost non-existent except at the buccal base of the hypoconid.

NAP XV 76'08, a well preserved left P4 shows an incipient wear facet on its lingual wall, affecting part of the paracone and the metastyle (Fig. 2-2). The presence of a well-formed parastyle is notable. The protocone is slightly displaced posteriorly with a well-formed conical cuspid. The basal cingulum is continuous but weak buccally and strong lingually. NAP XV 382'08, a well-preserved right M1, is a subtriangular, quite long tooth (Fig. 2-3). The paracone is somewhat taller and larger than the metacone, and its apex shows a horizontal wear facet that extends onto the posterior crista. The lingual cingulum is weak. There is a well-defined parastyle which shows a contact facet with the P4. The trigone valley is shortened with respect to the lingual wall of the buccal cusps, and is delimited by the well-developed metaconule and a large, globose protocone, which continues lingually without separating from the lingual cingulum which is only well marked in the zone between the metaconule and protocone. Three clear wear facets affect 1) the metacone, especially at the junction with the base of the metacone and at its apex 2) the central valley of the trigone extending onto the inner wall of the protocone, and 3) the base of the junction between the protocone and paracone. NAP XV 180'08 is a left M1 in which the external part has split away almost vertically such that only the lingual parts of the paracone and metacone are preserved. There is a clear, well-developed, metaconule and a sharp separation between the protocone and the lingual cingulum. The wear facets are similar to the ones on the specimen described above. NAP XV 98'07, a right M1, is smaller than the molars described above, and has lost the enamel in the area of the parastyle and metastyle (Fig. 2-4). The buccal cingulum is quite well marked but remains weak. The rest of the morphology is similar to the teeth described above, although occlusal wear is more advanced in the zone of the metaconule and the trigone valley. The main difference from the molars described above concerns the lingual cingulum which is well-formed and clearly separated from the protocone. NAP XV 146'08 and NAP XV 127'07 are left and right M2s respectively, both of which are heavily worn. They differ from the M1 by their more rectangular occlusal outline without marked narrowing of the area of the trigone. The trigone cusps appear to be quite low, at least in comparison with those of the M1.

NAP IX 14'02, right calcaneum (Fig. 3). The size and morphology of the calcaneum indicate that it is close to that

of *Cynelos lemanensis*, described and figured by Ginsburg (1977) from Saint Gérand-le-Puy, France. The fibular tuberosity is less well-developed than in this species, but this could be due to the state of preservation, which is slightly abraded as is the dorsal part of the *tuber calcanei*. The facet for the cuboid is short and ovoid in outline, differing from the subtriangular outline seen in *Amphicyon major* (Ginsburg, 1961, Fig. 15, 2). This difference could be related to the lesser medial lateral extension of the *sustentaculum tali*. Overall, the articular zone for the talus in the Napak calcaneum indicates a lesser degree of plantigrady than was present in *Amphicyon major* (Fig. 4). Comparison with the calcaneum of *Afrocyon ginsburgi* (= *Ysengrinia ginsburgi*) from Arrisdrift (Morales et al., 2003, Pl.4, Fig. 3) show that the Napak specimen is quite a bit smaller, about 20% smaller in its maximum dimension (proximo-distal length) but morphologically close to it; both share the ovoid outline of the cuboid articulation, which is quite deep, and a small medio-lateral development of the *sustentaculum tali*. Indeed, apart from the size difference, the two specimens are closely similar (Fig. 4).

Comparison with Napak I

The new material from Napak XV adds to our knowledge of the species *Hecubides euryodon*, defined by Savage (1965) on the basis of fossils from Napak I, especially regarding the mandible and lower dentition which was less well known than the upper teeth. The mandible from Napak XV is the first known adult specimen of the species and allows us to obtain more precise information regarding the dentition of *H. euryodon*, which has four relatively small premolars, separated from each other by diastemata. The mandible is noticeably elongated and it suggests that the rostral part of the skull of *H. euryodon* was elongated. The lower molars, especially the m1, are close to the material from Napak I, in particular NHM M 19085 (paratype of the species), which shares the strong development of the metacanid, the barely distinguishable entoconid that is essentially a peripheral cristid, and the overall bunodont aspect of the tooth. The upper teeth from Napak XV are close in dimensions to those in the holotype maxilla (M 19084) and show no clear morphological differences, apart from those mentioned in the discussion concerning the M1, NAP XV 382'08, which has lingual morphology which is somewhat divergent from other specimens from the same locality, and different from the molars from Napak I, in that the separation between the protocone and lingual cingulum is clearly marked. Another interesting difference in our opinion, is the stronger development of the parastyle in the P4 from Napak XV compared with the fossils from Napak I. Morales et al. (2007) described additional material of this species from Napak I including upper and lower deciduous teeth and an unworn molar. In conclusion, the forms from Napak I and Napak XV can be classified in the same species without any difficulty. Schmidt-Kittler (1987) described various specimens from other localities in the Lower Miocene of



Fig. 3.- *Hecubides euryodon* from Napak. NAP IX right calcaneum. 1) lateral view. 2) plantar view. 3) medial view. 4) dorsal view. 5) distal view. 6) proximal view.

East Africa and identified them as *Cynelos euryodon*. Among the fossils he studied were a m₂ from Napak I (NAP-1), close in dimensions and morphology to NAP XV 162'08, the two molars lacking a paraconid, the trigonid valley being high and small, and the talonid narrower than the trigonid.

In addition, Schmidt-Kittler (1987) reported the presence of this species at several other lower Miocene localities in Kenya including Rusinga and Songhor, as already noted by Savage (1965) and at Chamtwara. Schmidt-Kittler (1987) commented on the homogeneity of the African fossils when compared to the greater morphological diversity which is evident in European species of *Cynelos*, and he noted that the observed differences in the teeth from the African localities are small and could be related to differences in geological age. In the present state of our knowledge this inference appears to be correct, and although there are differences in size, in particular the small m₁ from Songhor (KNM SO-5668) or the greater dimensions of the m₁ Napak IV (HMV-5830), most of the remains are remarkably homogeneous. The same is indicated by the morphology, the few differences observed in a single locality such as among the M₁s at Napak XV, or the M₂s at Chamtwara (Schmidt-Kittler, 1987) being of minor significance. Like the variation in dimensions, the morphological variation within a single locality could be extrapolated to different localities, including the presence of a relatively strong parastyle in the P₄ from Napak XV, contrasting with the weaker or incipient parastyle in the P₄ from Napak I. More material is required to demonstrate that the

range of morphometric variation observed in the dentitions attributed to *Hecubides euryodon* might exceed species level variation.

Comparison with *Cynelos lemanensis*

Whilst the homogeneity of *Hecubides euryodon* appears to be clear at the species level and is now better documented, the validity of the genus *Hecubides* has been doubted on several occasions, with different authors synonymising it with *Cynelos*. Savage (1965) included *Amphicyon lemanensis* in his new genus, but the same year, Kuss (1965) revalidated



Fig. 4.- Comparison of the calcaneum of Amphicyonidae, dorsal view 1) *Amphicyon* sp. from Barajas 17 (Spain). 2. *Hecubides euryodon* from Napak NAP IX. 3) *Afrocyon ginsburgi* from Arrisdrift. The images are brought to the same size for ease of comparison.

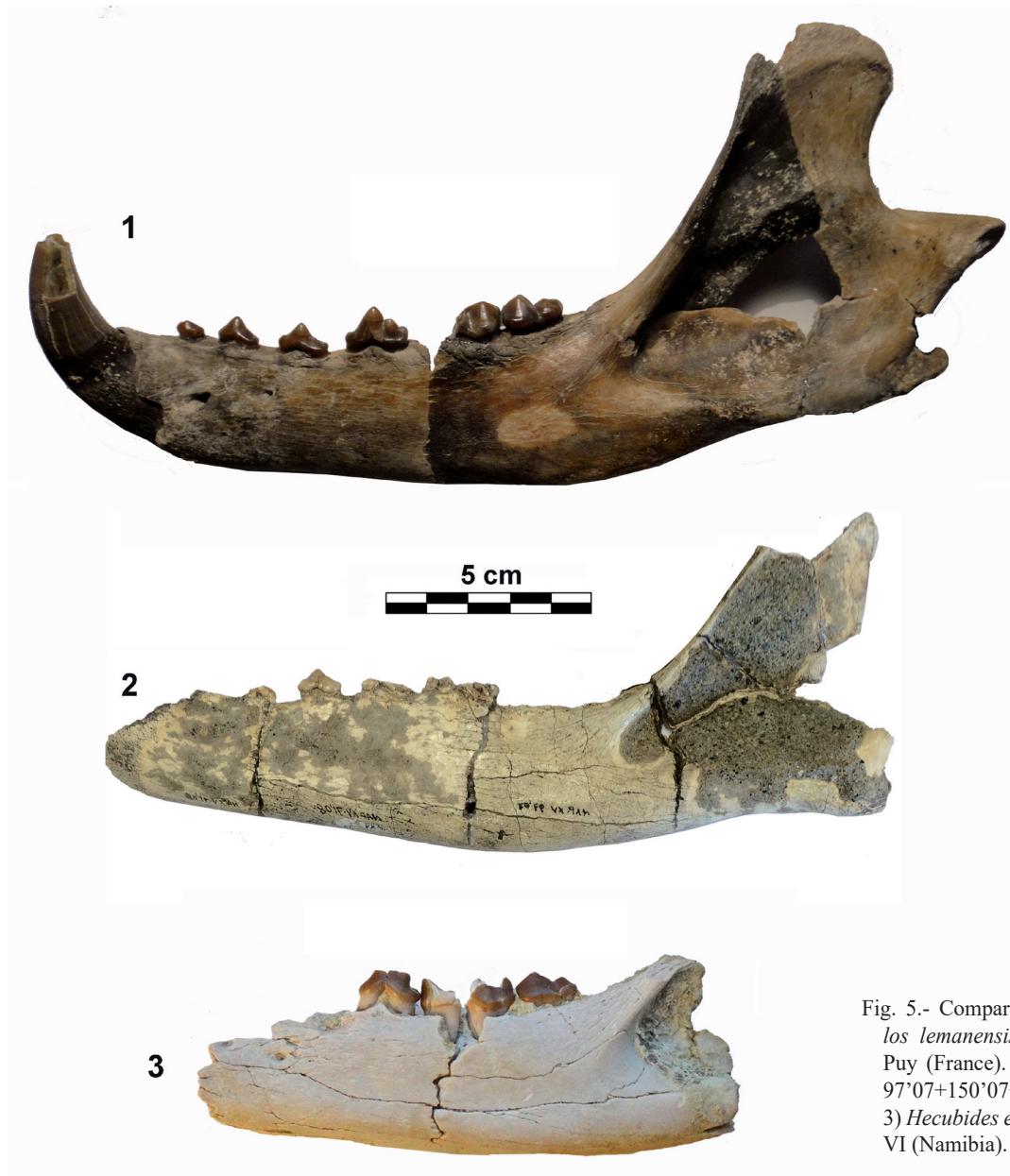


Fig. 5.- Comparison of the mandibles of 1) *Cynelos lemanensis* (SG 490) from Saint-Gérard-le-Puy (France). 2) *Hecubides euryodon* (NAP XV 97°07'+150°07'+91°08') from Napak XV (Uganda). 3) *Hecubides euryodon* (GT 35°15') from Grillental VI (Namibia).

(reutilised) the genus *Cynelos* Jourdan (1862) for the species *A. lemanensis* Pomel (1846). On this basis the combination *Cynelos euryodon* employed by Schmidt-Kittler (1987) for the African forms seemed to be beyond discussion. This was also the opinion supported by more recent authors such as Morlo *et al.* (2007) and Werdelin and Peigné (2010). In contrast Morales *et al.* (2007), Morales and Pickford (2008) and Morales *et al.* (2010) have used the *Hecubides* for these first African amphicyonids.

Hecubides euryodon is extraordinarily similar in dimensions to *Cynelos lemanensis*, at least as far as the dentition is concerned, and very few molars fall outside the range of variation known for the latter species in its type locality (Saint-Gérard-le-Puy, France), as can be observed in figures 5 and 6. The two species are longirostral with gracile and elongated mandibles. The anterior premolars (*p*1-*p*3) are reduced and separated from each other by diastemata. The large dimen-

sions of the second molars (*M*2 and *m*2) with respect to the first ones (*M*1 and *m*1) is similar in the two forms (Fig. 6), and apart from other considerations is a solid indication of a close relationship between them, especially if we consider that the tendency to broaden the crushing molars is a derived character of the Amphicyonids, less common than the reduction of the post-carnassial molars. There are thus sufficient arguments to unite the two genera and to support the view that they are synonyms. Nevertheless some morphological characters indicate differences between these two species, in particular the incipient development in *H. euryodon* of a parastyle in the *P*4, starting from the union of the anterior crista of the paracone with the cingulum (NAP XV 76°08'). In addition the African species shows a clearly defined protocone. The *M*1 of *H. euryodon* shows a clear reduction of the protoconal zone, such that the protocone cingulum is almost central and very reduced, whereas in *Cynelos lemanensis* the protoconal

area is less reduced and is more subquadrate. This fact is not evident in the figure published by Savage (1965, Pl. 5), probably due to an effect of light and shadow. In NAP XV 382'08 it is more than clear. However, it should be pointed out that *Cynelos piveteaui* Ginsburg (1966) shares with *H. euryodon* some of these features, in particular the narrowing of the protoconal area in the M1 and a better defined protocone in the P4. Nevertheless, it differs from *H. euryodon* by the greater development of the buccal cingula, and by the greater dimensions and robusticity of the P4, in which there is not a clearly defined parastyle. In the lower dentition, the differences are fainter, apparently in *H. euryodon* the hypoconid of the m1 seems to be somewhat more strongly developed, such that the lingual part of the talonid is narrower. Likewise the m2 of *H. euryodon* possesses a more reduced talonid, practically occupied by the hypoconid while in *C. lemanensis* the talonid is broader and possesses a relatively strong entoconid. Furthermore *C. lemanensis* presents a strong paraconid, equal to that of *C. piveteaui*, a cuspid that has been lost in *H. euryodon*. As has been pointed out, it is possible that the two genera were closely related, but the differences, although always difficult to evaluate in a family in which there is remarkable dental homogeneity (with some exceptions), tend to validate the independence of *Hecubides*. This is especially so when younger forms, some of which have also been included in *Hecubides* (or by some authors in *Cynelos*), the case with *H. macrodon* or *Hecubides* sp. from Wadi Moghara (Savage, 1965; Morlo et al., 2007), being more divergent from the standard morphology of *Cynelos*, as we discuss below, but showing closer affinities with *Hecubides*.

2.2. New material from Grillental VI

Locality: Grillental VI, Sperrgebiet, Namibia (Data about locality and fauna in Pickford and Senut (2008)).

Age: Early Miocene (Faunal Set I, ca 20 Ma).

Description

GT 35'15 is a left mandible containing p4-m2 and the alveoli of p3 and m3 (Fig. 7). The ascending ramus is broken off. The horizontal ramus is deep, and anteriorly shows a mental foramen, probably positioned beneath the p2 (which is not preserved) and the masseteric fossa is extensive and deep in its most posterior part. The specimen is close in dimensions and morphology to *Hecubides* from Napak V (Fig. 6, Table 2). The p3 has two roots and is separated from the p4 by a diastema. The p4 is damaged at its apex, posteriorly it is enlarged and possesses a well-developed posterior cusp and the main cusp would have been quite tall. The m1 is poorly preserved, retaining the antero-lingual part of the paraconid, the base of the protoconid and much of the talonid, in which a large hypoconid can be seen in a lingual position, and a crestiform entoconid. The m2 is broad with a short talonid. The protoconid is well-developed and is taller than the meta-

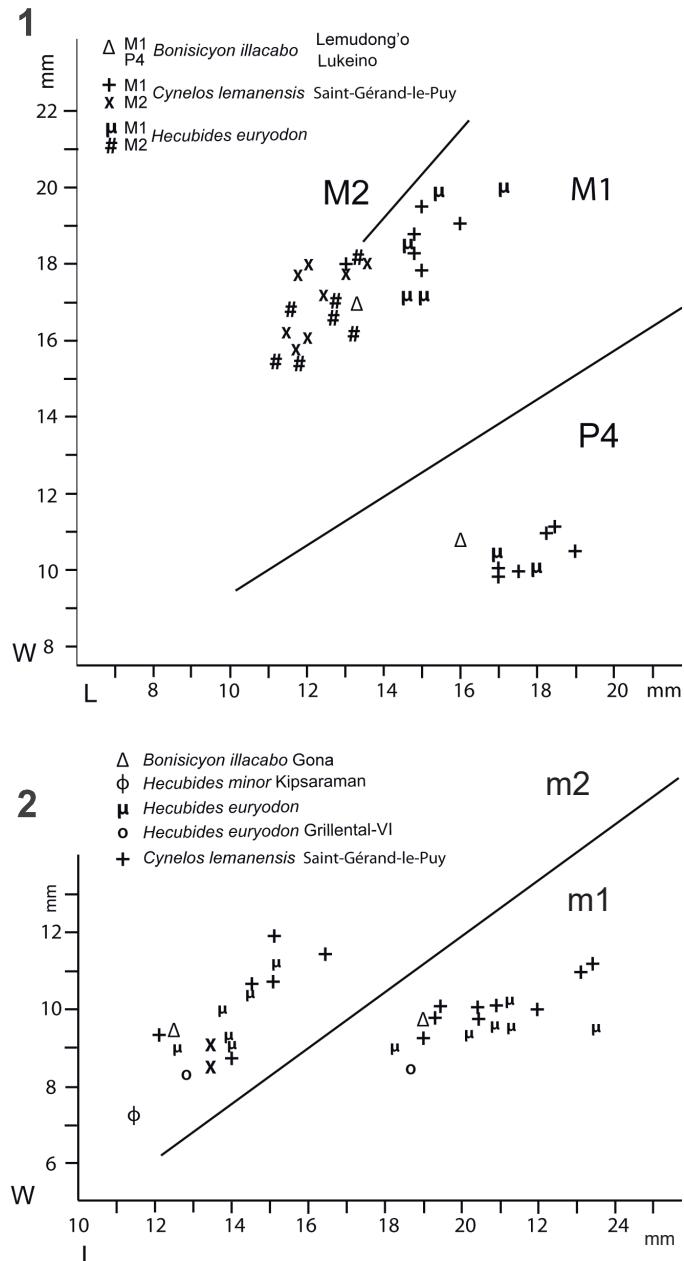


Fig. 6.- Bivariate plots of the upper teeth (1) and lower teeth (2) of small Amphicyonidae from Napak and from other African localities.

conid. There seems not to have been a metaconid. There also seems to be no paraconid, although the antero-lingual corner of the tooth is missing. The valley in front of the trigonid is small and is bordered anteriorly by a subtle cingulum. The talonid is dominated by a large hypoconid, and in the lingual margin, in the best preserved part, the beginning of a crest in the position of the entoconid can be observed. The posterior margin of the talonid is narrowed in its lingual part. There is a relatively big alveolus for the m3 in the jaw.

Comparisons

The new amphicyonid mandible from Grillental VI is the most complete specimen found in the early Miocene localities of the Sperrgebiet (excluding the site of Arrisdrift). In

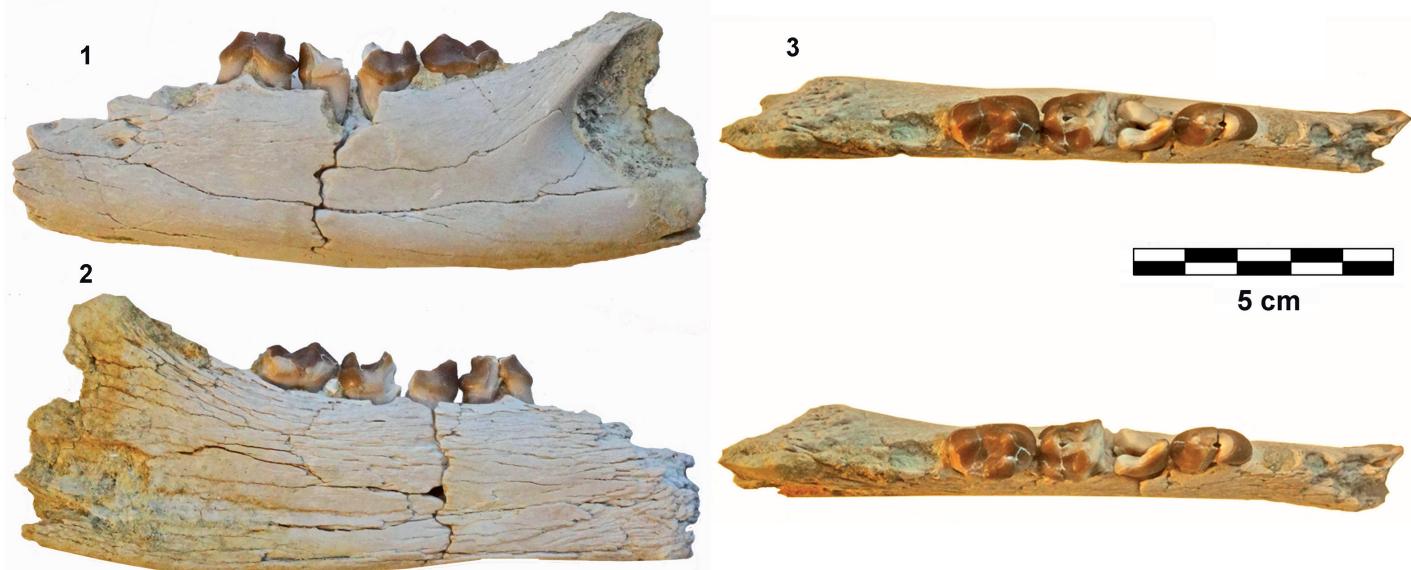


Fig. 7.- *Hecubides euryodon* from Grillental VI. GT 35'15, left mandible with p4-m2. 1) buccal view. 2) lingual view. 3) stereo occlusal view.

effect, in the sites of Langental, Elisabethfeld, Fiskus and Grillental amphicyonids were known, but only by post-cranial elements, save for an upper canine from Langental (LT 164'98). For this reason, the amphicyonids from the area were attributed to *Ysengrinia* sp. (Morales et al., 2008). Even though the preservation of the Grillental mandible is not excellent, it permits us to classify it as *Hecubides euryodon* for the following reasons; the dimensions of the jaw and of the teeth preserved in it, which are close to the smallest individuals of the species, represented by an m2 from Napak XV (Nap XV 162'08) and an m1 from Songhor (KNM SO 5668); the p4 is close to a specimen described by Morales et al. (2007) from Napak I, sharing the posterior expansion and the posterior accessory cusplet; and the m2, without paraconid and with a short and postero-lingually narrowed talonid; all of which are characteristic of the taxon. It is likely that most of the post-cranial bones from Langental, Elisabethfeld and Grillental can also be attributed to *Hecubides euryodon* on the basis of their dimensions which are compatible with the jaw. This species is smaller than *Afrocyon ginsburgi* from Arisdrift (Morales et al., 2003).

3. Systematic approach to African Amphicyonidae not *Hecubides*

A classic problem with the palaeontology of carnivores is the relation between the upper and lower dentitions especially when there is scarce material, and/or which may belong to more than one species of the group, a situation which is quite common among the Amphicyonidae. The criterion of size on its own, with some exceptions, is difficult to apply on account of the presence of sexual dimorphism and bimodality, and because there is often overlap in dimensions of different species (Dehm, 1950). Additionally, as correctly one review-

er (L.W.) has pointed out “several of the type specimens of African Amphicyonidae are limited in scope or poorly preserved”. For these reason the use of genera as *Afrocyon* and *Myacyon* poses serious problems. Conscious of this reality, however, we have preferred to use these existing names. The new material from Gebel Zelten described by Morales et al. (2010) in some ways compensates the poor preservation of the *Afrocyon burolleyi* holotype. The case of *Myacyon* is completely different because it is not easy to find a holotype with quality to name a new genus, and restrict *Myacyon domjabir* to the type locality.

SUBFAMILY Amphicyoninae Haeckel, 1866

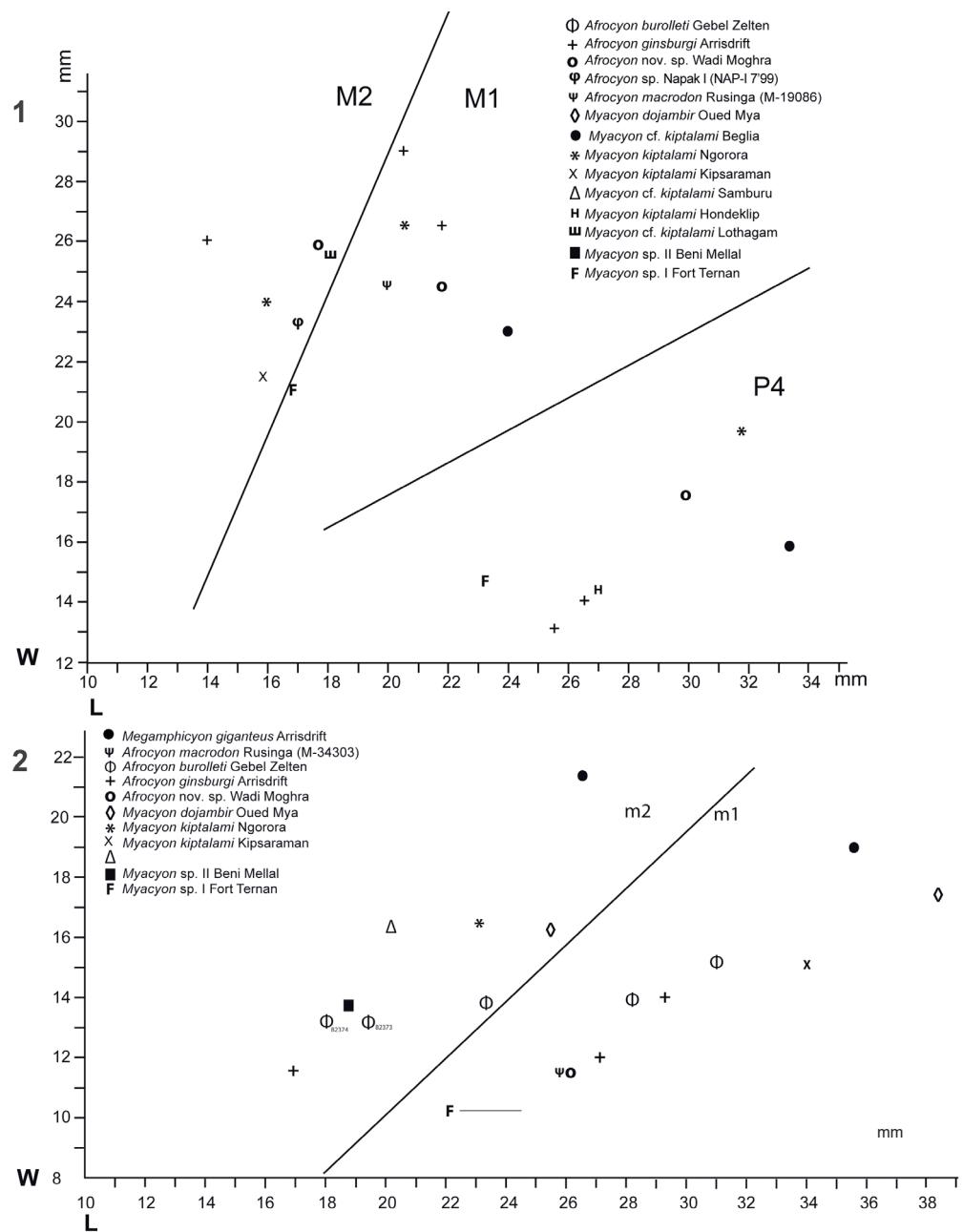
Genus: *Afrocyon* Arambourg, 1961

Type species: *Afrocyon burolleyi* Arambourg, 1961

Diagnosis: Werdelin and Peigné (2010).

Differential diagnosis: Apart from its smaller dimensions, *Afrocyon* differs from *Amphicyon major* and *Megamphicyon giganteus* by its clearly more hypercarnivorous dentition, which is more sectorial, the p4 is reduced, and the talonids of m1 and m2 are reduced although the hypoconid is more developed. Similarly, in the m2 of *Afrocyon burolleyi* (NHM M 82374) the morphology is clearly more primitive than it is in *Amphicyon major*, as revealed by the retention of the paraconid, the taller and larger dimensions of the protococonid with respect to the metaconid, and its posterior position. Comparable differences apply to *Megamphicyon giganteus*, a species with larger premolars with barely any gaps between them. *Afrocyon* differs from *Hecubides* Savage (1965), not only by its greater dimensions, but mainly by its markedly more hypercarnivorous dentition. Finally, *Afrocyon* differs from *Myacyon* by the lesser developed carnassials (P4/m1), and the minor size of the parastyle in the P4.

Fig. 8.- Bivariate plots of the upper teeth (1) and lower teeth (2) of medium-large Amphicyonidae from African localities.



Afrocyon burolleti Arambourg, 1961

Type locality: Gebel Zelten, Libya.

Age: Early/Middle Miocene, ca. 17-15 Ma.

Holotype: MNHN 1961-5-7, left mandible with abraded cheek teeth (p4-m3).

Remarks: New material was described by Morales *et al.* (2010) from Gebel Zelten. NHM M-82373, left mandible containing well preserved p4-m2, the alveoli for m3, p3 and p2 (Fig. 8 and 9.1). NHM M-82374, left m2.

Afrocyon ginsburgi (Morales *et al.*, 1998)

1978 *Amphicyon cf. steinheimensis* Hendey
1998 *Ysengrinia ginsburgi* Morales *et al.*

2003 *Ysengrinia ginsburgi* Morales *et al.*

2010 *Ysengrinia ginsburgi* Werdelin and Peigné

Type Locality: Arrisdrift, Namibia.

Age: Early Miocene, ca. 17.5-17 Ma.

Holotype: AD 133, left mandible.

Diagnosis: In Morales *et al.* (1998).

Remarks: The presence of a large M2 in this species excludes their classification as *Ysengrinia*. Even though the maxilla of *Afrocyon ginsburgi* AD 604'94 (Fig. 9.5) does not have an M2, the existence of an edentulous maxilla (Morales *et al.*, 2003), which shows alveoli with appropriate dimensions, indicates that the M2 in the Namibian species was not reduced (Fig. 9.6), at least to the stage observed in the type species of the genus, *Ysengrinia gerandiana* (Viret, 1929; Ginsburg,

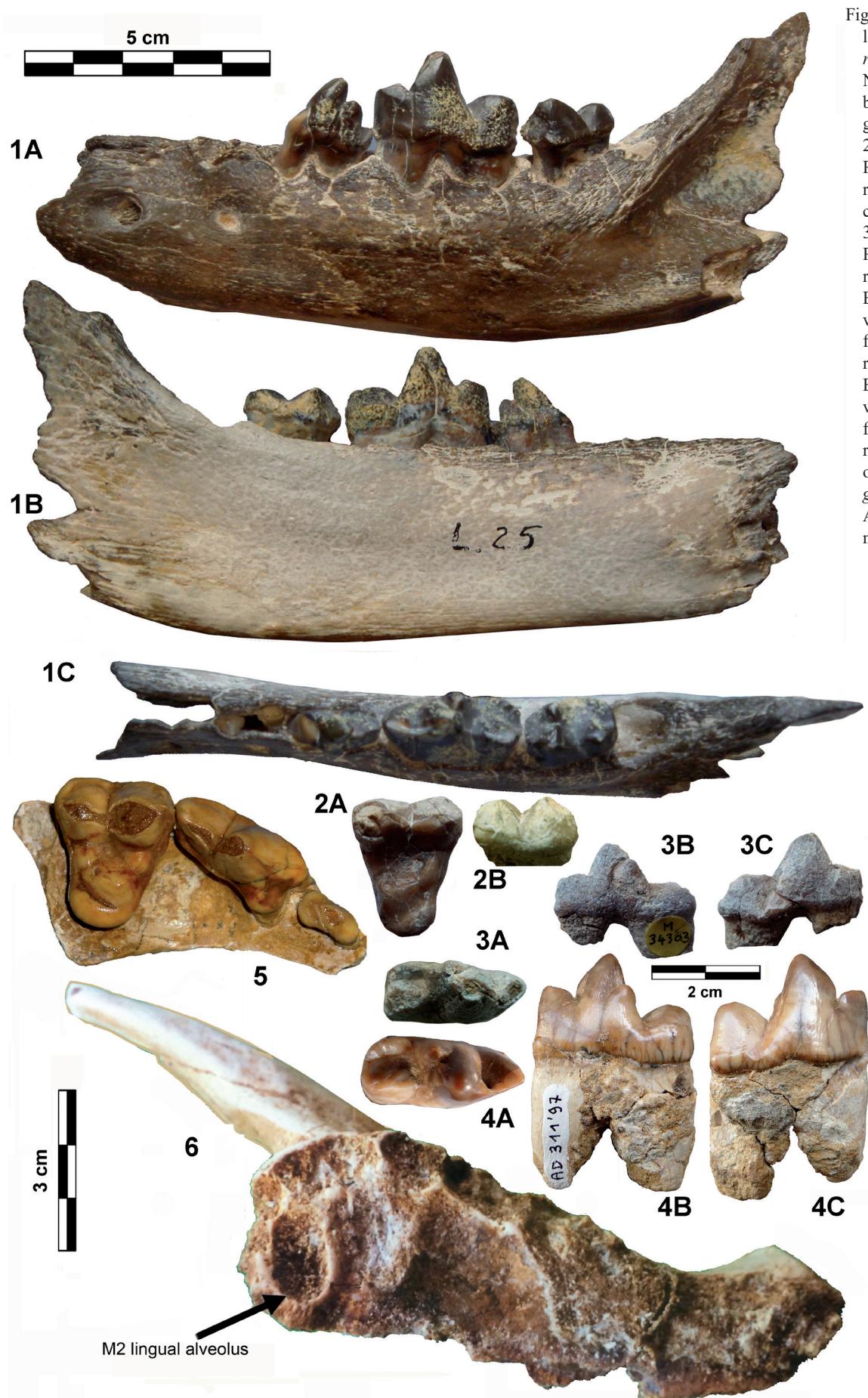


Fig. 9.- *Afrocyon* from African localities. 1. *Afrocyon burolleti* from Gebel Zelten. NHM M-82373, left mandible. A) buccal view. B) lingual view. C) occlusal view. 2) *Afrocyon macrodon* from Rusinga NHM M-19086, right M1 (holotype). A) occlusal view. B) buccal view. 3) *Afrocyon macrodon* from Rusinga NHM M-34303, right m1. A) occlusal view. B) lingual view. C) buccal view. 4. *Afrocyon ginsburgi* from Arrisdrift. AD 311'97, right m1. A) occlusal view. B) lingual view. C) buccal view. 5. *Afrocyon ginsburgi* from Arrisdrift. AD 604'94 right maxilla with M1-P3 in occlusal view. 6. *Afrocyon ginsburgi* from Arrisdrift. AD 606'94 edentulous maxilla in occlusal view.

1966). *Afrocyon ginsburgi* differs from *A. burolleti* by its slightly smaller dimensions, and by the reduction of the m2. The only m2 preserved at Arrisdrift is somewhat smaller than the specimens from Gebel Zelten (Morales et al., 2010), and they differ in morphology, in particular by the strong elongation of the talonid. The differences between the material from Arrisdrift and Gebel Zelten are minor when compared with the m1s. However, this tooth is quite homogeneous among the African amphicyonids. Therefore, we are in the presence of a group of forms that are characterised by: significantly larger dimensions than *Hecubides euryodon*; lower carnassial relatively short with a vertical paraconid and strong hypoconid (Figs. 1, 3, 4), unreduced second molars, and a tendency to elongate the P4 which possesses an incipient parastyle.

Afrocyon macrodon (Savage, 1965)

1987 *Cynelos macrodon* Schmidt-Kittler
2010 *Cynelos macrodon* Werdelin and Peigné

Type Locality: Site 31, Rusinga, Kenya.

Age: Early Miocene, 18-17 Ma.

Holotype: NHM M-19086 left M1.

Diagnosis: In Savage (1965).

Measurements in Table 2.

Remarks: The greater dimensions of one M1 from Rusinga (Fig. 9.2), compared to the dentition classified as *Hecubides euryodon* from the same locality, prompted Savage (1965) to define a distinct species *Hecubides macrodon*, which Schmidt-Kittler (1987) considered to be ?*Cynelos macrodon*. This species was cited by Morales and Pickford (2008) at Kipsaraman, Kenya, on the basis of an isolated M2, now attributed to *Myacyon kiptalami*, a species also present in the site. A m1 found at Rusinga (NHM M-34303) not figured nor described by Savage (1965) is also attributed to this species (Fig. 9.3). *Afrocyon macrodon* could be conspecific with *Afrocyon burolleti*, but the limited material does not permit precise comparisons.

Afrocyon nov. sp.

2007 *Cynelos* nov. sp. Morlo et al.
2010 *Cynelos* sp. Werdelin and Peigné.

Type Locality: Wadi Moghara.

Age: Early Miocene, 18-17 Ma.

Remarks: Morlo et al. (2007) classified four teeth collected at Wadi Moghara, Egypt, as *Cynelos* sp. nov., the dimensions of which are almost the same as those of *Afrocyon macrodon* from Rusinga, at least as concerns the m1 and M1 represented in both localities. There are no great differences in the morphology of these molars, in the m1 the hypoconid is voluminous and occupies the greater part of the talonid, but

the m1 of *Afrocyon burolleti* and *Afrocyon ginsburgi* are in these respects similar. The M1 from Wadi Moghara is a bit more triangular and with a marked narrowing in the protocanal area, as occurs in *Hecubides euryodon*, but also as in the holotype of *A. ginsburgi* (Morales et al., 1998). Nevertheless, the lengthening of the P4 is notable, and by this feature and the presence of a clearly defined parastyle, it differs from the Arrisdrift species, the P4 of which is short with only an incipient parastyle. Finally, the presence at Wadi Moghara of a large M2 (Fig. 8), a feature which it shares with at least *Hecubides euryodon*, *Afrocyon ginsburgi*, and *Myacyon kiptalami* (= *Agnotherium kiptalami*). However, seen in the light of African Amphicyonidae, neither *Ysengrinia* nor *Agnotherium* appear to be sustainable as valid genera for these African species. *Afrocyon* nov. sp. from Wadi Moghara cannot be differentiated from *A. macrodon*, nor from *A. burolleti*, but its upper teeth show differences from those of *Afrocyon ginsburgi* in particular the lengthening of the P4, a tendency which is fully developed in more modern African amphicyonids classified as *Myacyon* (Fig. 8).

Afrocyon sp.

Locality: Fiskus, Namibia.

Age: Early Miocene (Faunal Set I, ca. 20 Ma).

Description

FS 17'03 right calcaneum (Morales et al., 2008, Fig. 3, table 4) is clearly larger than the specimen from Napak XV described as *Hecubides euryodon*, and is close in dimensions to *Afrocyon ginsburgi*, and while its poor preservation does not permit precise comparisons, it does indicate the presence of a second species of Amphicyonidae in the Sperrgebiet localities, which can be named *Afrocyon* sp.

Locality: Napak 1.

Age: Early Miocene (Faunal Set I, ca. 20.5 Ma).

Description

NAP-I 7'99 is a left M2 (Fig. 2.6) considerably larger than the homologous tooth of *Hecubides euryodon* (Table 2). It is a low-crowned tooth, almost completely surrounded by a cingulum, especially strong postero-lingually. The paracone is slightly taller than the metacone, the protocone is large and displaced mesially. Morphologically the tooth is very close to the M2 from Wadi Moghara identified by Morlo et al. (2007, Fig. 4-D). Nevertheless, with only one M2 available it is difficult to make an accurate identification and, as in the case of Grillental-VI we propose to attribute this tooth to *Afrocyon* sp., emphasizing the presence of two amphicyonid species in the Early Miocene deposits of Napak.

Genus: *Myacyon* Sudre and Hartenberger, 1992

Type species: *Myacyon dojambir* Sudre and Hartenberger, 1992

Fig. 10.- Caniformia indet. aff Amphicyonidae. KNM LU 227, right P4. 1) stereo occlusal view. 2) stereo buccal view. 3) stereo lingual view.



Diagnosis: In Sudre and Hartanberger (1992); modified by Werdelin and Peigné (2010).

Myacyon dojambir Sudre and Hartenberger, 1992

2010 *Myacyon dojambir* Werdelin and Peigné

Type Locality: Oued Mya, Algeria.

Age: Late Miocene, ca. 11.2-9 Ma.

Holotype: Right mandible with m1-m2, and m3 not yet erupted.

Diagnosis: In Sudre and Hartanberger (1992).

Remarks: *Myacyon dojambir* was described by Sudre and Hartenberger (1992) from the Late Miocene of Oued Mya 1, on the basis of a mandible containing m1-m2, poorly figured, approaches the dimensions of large *Megamphicyon giganteus* from Europe. It differs from them by the greater strength of the metaconid in the m1, a talonid narrower than the trigonid in the m2, as well as its smaller dimensions with respect to the m1.

Myacyon kiptalami (Morales and Pickford, 2005)

1997 *Agnotherium* sp. Pickford and Senut

2005 *Agnotherium kiptalami* Morales and Pickford

2008 *Agnotherium* cf. *kiptalami* Morales and Pickford

2010 *Agnotherium kiptalami* Werdelin and Peigné

Type Locality: 2/10, Kabarsero, Ngorora Formation, Kenya. Other localities: Kipsaraman, Kenya; Hondeklip Bay, South Africa.

Age: Middle Miocene, 16-12 Ma.

Holotype: KNM BN 488, snout broken off behind the second molars.

Diagnosis: In Morales and Pickford (2005).

Remarks: We mentioned above that the presence of a large M2 in several African forms as *A. ginsburgi* excludes their classification as *Ysengrinia*, and that the same criterion could apply to the forms classified as *Agnotherium* which retain large M2s, the case with *Agnotherium kiptalami* from the Ngorora Formation (Morales and Pickford, 2005). *Agnotherium* was, and is, a genus which is difficult to define, because it was erected on the basis of an isolated m1 (Kaup, 1832), and the reconstruction of the upper dentition by Kuss (1962) on the basis of specimens from Frohnstetten, was questioned by Kurtén (1976) which caused much confusion by emphasizing that the reduction of the molars, in comparison to the size of the carnassial was not excessively marked. The problem is not solved transferring the Frohnstetten form to *Tomocyon* or *Thaumastocyon* as proposed by Kurten (1976), because the holotype of *Agnotherium* is indistinguishable of the m1 of *Thaumastocyon bourgeoisi* (Stehlin and Helbing, 1925) a genus which shows a reduction of the molars which is notable at least since the Middle Miocene, which also is present with *Thaumastocyon dirus* from the Upper Miocene of Los Valles de Fuentidueña (Ginsburg *et al.*, 1981). However, ever since the Early Miocene, first with *Ysengrinia* and then with *Thaumastocyon* plus *Agnotherium* and *Tomocyon*, this group of hypercarnivorous amphicyonid shows a strong tendency for the reduction of the molars, which makes it incompatible that forms such as that described from Ngorora can be classified in *Agnotherium*. The presence of a large m2 in the

Ngorora species (Morales *et al.*, 2010) adds to the arguments in favour of a different generic identification for this form. *Agnotherium* has also been reported from Kipsaraman, on the basis of a mandible and a canine, as *Agnotherium cf. kiptalami* (Morales and Pickford, 2008). This material, in line with what was written above, could well be associated with the M2 identified as *Hecubides macrodon* from the same locality and included in this species. The P4 from Hondeklip Bay described by Pickford and Senut (1997) as *Agnotherium* sp. can also be attributed to this species (Morales and Pickford, 2005).

Myacyon cf. kiptalami (Morales and Pickford, 2005).

1976 *Agnotherium cf. antiquum* Kurten

2003 Amphicyonidae sp. A. Werdelin

2005 Amphicyonidae indet. Tsujikawa

2010 *Agnotherium cf. antiquum* Werdelin and Peigné

2010 Amphicyonidae sp. A Werdelin and Peigné

2010 Amphicyonidae indet. Werdelin and Peigné

Localities: Beglia Fm., Tunisia. Samburu and Lothagam, Kenya.

Age: Middle/Late Miocene, 13-6 Ma.

Remarks: Kurtén (1976) included in *Agnotherium antiquum* a fragment of maxilla from the Beglia Formation, Tunisia, with a long P4 and alveoli of the M1 which shows that the tooth must have been quite big, in particular its length. The species from Beglia are among the largest in Africa, and morphologically is close to the species of Ngorora.

The mandible with m2 described by Tsujikawa (2005) from the Samburu Formation has slightly smaller dimensions but very similar morphology to the m2 described from Ngorora (Morales and Pickford, 2010). This m2 is also close to *M. dojambir* but somewhat more gracile, the cingulum of which is barely developed, a difference from *M. dojambir*. This determination should be extended to the M2 from Lothagam described by Werdelin (2003) as Amphicyonidae species A, which size is close to M2 from Ngorora species,

Myacyon sp. I

2005 *Agnotherium* sp. Morales and Pickford

2009 *Agnotherium* sp. Werdelin and Simpson

2010 *Agnotherium* sp. Werdelin and Peigné

Locality: Fort Ternan, Kenya.

Age: Middle Miocene, ca. 14 Ma.

Remarks: *Agnotherium* has also been described from Fort Ternan (Morales and Pickford, 2005; Werdelin and Simpson, 2009). As in other sites the material is scarce, a damaged m1 the size of which could correspond to species of *Afrocyon*. It preserves a strong metaconid, already lost early in the Thaumastocyoninae, but the paraconid shows a strong anterior vertical cristid, a structure which is seen in m1s of

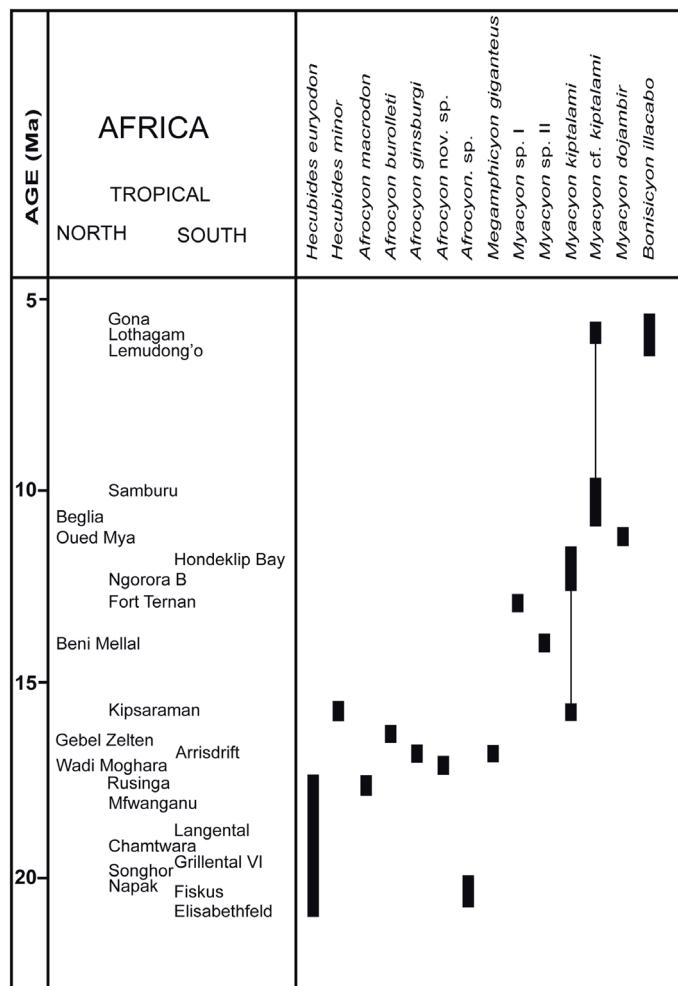


Fig. 11.- Biostratigraphy of African Miocene localities, with the temporal ranges of the diverse species of amphicyonids found therein.

Thaumastocyon. The M1 and P4 are relatively small, smaller than the measurements of species of *Afrocyon*. The presence of a parastyle in the P4 and the antero-posterior shortening of the protoconal area in the M1 are features present not only in *Afrocyon*, but also in the forms discussed in this section. Like the available material, the Fort Ternan amphicyonid could still be identified as *Afrocyon* sp., or could equally correspond to a small form of *Myacyon*.

Myacyon sp. II

1977 *Agnotherium cf. antiquum* Ginsburg

2010 *Agnotherium cf. antiquum* Werdelin and Peigné

Locality: Beni Mellal, Morocco.

Age: Middle Miocene, ca. 14 Ma.

Remarks: The morphology of the m2 de Beni Mellal is apparently close to that of *Myacyon dojambir* (Sudre and Hartenberger, 1992) with a short talonid and a robust cingulum but it is considerably smaller.

Genus: *Bonisicyon* Werdelin and Simpson 2009

Type species: *Bonisicyon illacabo* Werdelin and Simpson 2009

Diagnosis: In Werdelin and Simpson 2009.

Bonisicyon illacabo Werdelin and Simpson 2009

2003 Amphicyonidae species B. Werdelin

2007 *Simocyon* sp. Howell and García

2010 *Bonisicyon illacabo* Werdelin and Peigné

Type locality: Hamadi Das, Gona, Ethiopia

Holotype: HMD1/P11, right m1.

Age: Late Miocene, 6.5-5.3 Ma.

Remarks: *Bonisicyon illacabo* was erected by Werdelin and Simpson (2009) for a group of fossils from various localities, characterised by their small dimensions and their more recent age (end Miocene) (Fig. 6). The holotype is an m1, from Gona (Ethiopia), similar in size to *Hecubides euryodon*, which however possesses a metaconid which is almost entirely reduced and quite a broad talonid and thereby differs from the latter taxon. From the same zone came a poorly preserved m2 which is markedly different in its squarer talonid from specimens of *Hecubides euryodon*. However, the M1 from Lemudong'o, Kenya, previously described as *Simocyon* sp., by Howell and Garcia (2007) and attributed to *Bonisicyon* by Werdelin and Simpson (2009) shows substantial differences from the M1 of *Hecubides euryodon*, in particular the strong reduction of the protoconal area, the almost perfectly semicircular morphology of the protocone in which the paraconule can barely be differentiated, and by the strong lingual cingulum.

With such scarce evidence it is difficult to determine the relationships to other African amphicyonids, and like *Hecubides minor* from Kipsaraman (Morales and Pickford, 2008), defined on the basis of an m2 which is smaller than that of *Hecubides euryodon* and *Bonisicyon illacabo*, these small forms need a better fossil record before a more plausible hypothesis about their phylogenetic relationships can be proposed.

Caniformia indet. aff. amphicyonidae

Morales et al. (2005) referred a right P4 (KNM LU 227) from the Lukeino Formation (Kenya) to *Plesiogulo praecocidens*. Although the presence of the genus *Plesiogulo* in this formation is certain, this P4 must be excluded from the genus, which would be represented by a lingual part of an M1 (BAR 1893'00). *Plesiogulo* was recently described from Lemudong'o (Kenya) and Adu Dora (Ethiopia) aged 5.5-6 Ma belonging to the new species *P. botori* Haile-Selassie et al. (2004). Morphologically the large mustelid from the Lukeino Formation accords better with this new species than with *P. praecocidens*.

The P4 from Lukeino (Fig. 10) presents an interesting association of morphological characters which clearly distinguishes it from *Plesiogulo* (and by extension from modern Mustelidae), such as the retention of a strong notch between the protocone and metastyle (loss of this notch is a derived feature of modern mustelids), as well as the reduction of the protocone, its relatively distal position and weak individualisation with respect to the paracone. The caniform morphology of this P4 seems beyond discussion, but its familial attribution is more problematic. The dimensions of the carnassial are close to those of *Hecubides euryodon*, although the tooth is more robust, in general it could correlate well with *Bonisicyon illacabo* (Fig. 6). However, the majority of the more modern Amphicyonidae, even though they present a strong reduction of the protocone of P4, it is rarely retracted. On the contrary in the Hemicyonidae the protocone of P4 is shifted distally, but not reduced, and soon increases in size. For this reason, the Lukeino form accords well with primitive species of the family Hemicyonidae, such as *Hemicyon garigan* or *Hemicyon stehlini* (Ginsburg and Morales, 1998). The Hemicyonidae are frankly rare in African faunas, but they occur in the Lower Miocene of Rusinga, where a P4 is known (Schmidt-Kittler, 1987), and near the Mio-Pliocene boundary, with the spread of *Agriotherium* (Morales et al., 2005), although the latter genus has a highly divergent P4 morphology compared to the Lukeino specimen. It is not reasonable to think of an alternative to Hemicyoninae, or by extension of Ursidae (which also possess highly derived P4). Similar morphology of the Lukeino P4 occurs in *Simocyon*, an Ailuridae which shows several dental convergences to Amphicyonidae, so much so that one of the molars (M1) attributed to *Bonisicyon illacabo* was originally identified as *Simocyon*.

The P4 of *Simocyon* has a morphological pattern which is close to that of the Lukeino tooth, the parastyle is variable, depending on the species, in *S. diaphorus* from Rudabanya, Hungary, it is practically absent (Werdelin, 2005), whereas in *S. batalleri* from Batallones, Spain, and other more modern species such as *S. primigenium* is well-developed (Peigné et al., 2005). The position of the protocone in *Simocyon* appears to be related to the development of the parastyle, such that in *S. diaphorus* from Rudabanya the protocone occupies a very anterior position, in front of the the anterior border of the paracone, although it certainly extended distally. In contrast, in *S. batalleri* and *S. primigenium* in which the parastyle is well-developed, the protocone is positioned more distally, but also front of the paracone, or which is the same, it starts developing at the level of the separation between the paracone and parastyle. As such, the Lukeino P4 does not correspond to any of these morphotypes, differing from that of *S. diaphorus* by the distal position of the protocone, and from *S. batalleri* and *S. primigenium* by the weak development of the parastyle. If we take into account the fact that until now there is no reliable record of Ailuridae in African faunas the hypothesis that the Lukeino P4 is related to this family seems improbable.

In summary, the Amphicyonidae hypothesis seems more plausible at the moment, two possibilities could give rise to this morphology; 1) from *Afrocyon-Myacyon*. In these forms the tendency for the P4 to develop parastyles could displace the protocone into a more distal position. Adaptation to a smaller size could be accompanied by regression of the parastyle, conserving the protocone in its distal position; 2) the Lukeino P4 could be related to Amphicyonidae in which the protocone of the P4 maintained its strong development, as in *Pseudarctos* and *Ictiocyon* (Ginsburg, 1999). It is evident that identification of the Lukeino P4 as an Amphicyonidae is likely, not only because of its morphology but also because of its dimensions and age, which are close to those of *Bonisicyon illacabo*.

4. Phylogenetic proximity

The available data about African amphicyonids are still insufficient for carrying out a rigorous analysis of their phylogenetic relationships. There are too many gaps and important questions without documentation. Nevertheless, the main aim of this contribution is to arrange the available information about this family in Africa (Fig. 11). The first conclusion that emerges is that there is a great deal of morphological homogeneity in the family in Africa, apparently confined to a single phylogenetic lineage, comprised of *Hecubides-Afrocyon-Myacyon*, with the exception of the large amphicyonid from Arrisdrift, identified as *Megamphicyon giganteus* (Morales et al., 1998) and the younger *Bonisicyon illacabo* Werdelin and Simpson (2009), the latter of which could be related to *Hecubides*, as discussed above.

It is clear that there is a strong resemblance between the first amphicyonids classified as *Hecubides euryodon* and the larger forms *Afrocyon* and *Myacyon*. The greater dimensions of *Afrocyon* can be related to morphological differences between the species of *Afrocyon* and *Hecubides*, in particular the stronger paracone in the M1 and the greater sectoriality of the m1 with a high and sharp trigonid. But above all, the great elongation of the P4 and to a lesser extent the m1, mark an important qualitative jump which allows us to separate *Hecubides* from *Afrocyon*. Relations within the genus *Afrocyon* are not resolved because of which we leave the specific status as it was. *Myacyon* is close to *Afrocyon*, but the tendency to elongate the carnassials, in the case of the P4 in addition developing a strong parastyle, led to some of these forms being previously related to *Agnotherium* (Kurtén, 1976; Morales and Pickford, 2005) but the retention of relatively large post-carnassial molars renders this proposal unlikely. As in the case of *Afrocyon*, the relation between the species attributed to *Myacyon* is not resolved, and only a better fossil record will yield a solution. Forms such as those from Fort Ternan and Beni Mellal may be included in the genus *Myacyon*, in spite of their dimensions being closer to those of *Afrocyon* for the reasons pointed out above, the m1 from Fort Ternan is quite derived with respect to the species of *Afrocyon* (on

the basis of this molar) and the m2 from Beni Mellal show undoubtedly morphological similarities to *Myacyon dojambir*, including the development of a strong buccal cingulum. Provisionally we call them *Myacyon* sp., in the hope of obtaining better documentation.

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