geodiversitas

2019 • 41 • 21

New Amphicyonids (Mammalia, Carnivora) from Moghra, Early Miocene, Egypt

Michael MORLO,
Ellen R. MILLER,
Katharina BASTL,
Mohamed K. ABDELGAWAD,
Mohammed HAMDAN,
Ahmed N. EL-BARKOOKY & Doris NAGEL

MUSÉUM
NATIONAL D'HISTOIRE NATURELLE
PUBLICATIONS SCIENTIFIQUES

art. 41 (21) — Published on 7 November 2019
www.geodiversitas.com

Couverture / *Cover* :
Made from the Figures of the article.

Geodiversitas est indexé dans / Geodiversitas *is indexed in:*
- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Physical, Chemical, and Earth Sciences®
- Scopus®

Geodiversitas est distribué en version électronique par / Geodiversitas *is distributed electronically by:*
- BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Geodiversitas* sont référencés par /
Articles and nomenclatural novelties published in Geodiversitas *are referenced by:*
- ZooBank® (http://zoobank.org)

Geodiversitas est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia, ***Zoosystema***, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Naturae***, ***Cryptogamie*** **sous-sections** ***Algologie***, ***Bryologie***, ***Mycologie.***

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

New Amphicyonids (Mammalia, Carnivora) from Moghra, Early Miocene, Egypt

Michael MORLO
Forschungsinstitut Senckenberg, Abt. Messelforschung, Senckenberganlage 25,
60325 Frankfurt am Main (Germany)
michael.morlo@senckenberg.de (corresponding author)
https://orcid.org/0000-0003-3956-7912

Ellen R. MILLER
Wake Forest University, Department of Anthropology,
Winston Salem, NC 27109-7807 (United States)
https://orcid.org/0000-0002-4942-4475

Katharina BASTL
Research group Aerobiology and Pollen information,
Department of Oto-Rhino-Laryngology, Medical University of Vienna
and Department of Palaeontology,
Universität Wien, Althanstrasse 14, 1090 Wien (Austria)
https://orcid.org/0000-0002-8200-9708

Mohamed K. ABDELGAWAD
Geology Department, Faculty of Sciences, Cairo University, Cairo (Egypt)
https://orcid.org/0000-0002-3229-3800

Mohammed HAMDAN
Ahmed N. EL-BARKOOKY
Geology Department, Faculty of Sciences, Cairo University, Cairo (Egypt)

Doris NAGEL
Department of Palaeontology,
Universität Wien, Althanstrasse 14, 1090 Wien (Austria)
https://orcid.org/0000-0002-8940-6351

Submitted on 12 December 2018 | accepted on 3 June 2019 | published on 7 November 2019

urn:lsid:zoobank.org:pub:F2985B60-626C-4FF6-8C0F-C62C34531199

Morlo M., Miller E. R., Bastl K., AbdelGawad M. K., Hamdan M., El-Barkooky A. N. & Nagel D. 2019. — New Amphicyonids (Mammalia, Carnivora) from Moghra, Early Miocene, Egypt, *in* Bonis L. de & Werdelin L. (eds), Memorial to Stéphane Peigné: Carnivores (Hyaenodonta and Carnivora) of the Cenozoic. *Geodiversitas* 41 (21): 731-745. https://doi.org/10.5252/geodiversitas2019v41a21. http://geodiversitas.com/41/21

ABSTRACT

We describe two large amphicyonid (Amphicyonidae, Carnivora) mandibles from Moghra, Early Miocene, Egypt. One of these represents a new species of *Cynelos* Jourdan, 1862, which is in the same size range as *C. macrodon* (Savage, 1965) and *C. ginsburgi* n. comb., but exhibits a relatively longer m1 paraconid blade. The other is allocated to *Amphicyon giganteus* (Schinz, 1825). Based on this new material the differences between *Cynelos*, *Amphicyon* Lartet in Michelin, 1836, and *Afrocyon* Arambourg, 1961 are clarified. We also reassign three (P4, M1, M2) of four isolated and unassociated amphicyonid teeth from Moghra, previously attributed to "*Cynelos* sp. nov." to *Amphicyon giganteus*. These teeth represent the first record of the upper dentition of *A. giganteus* from Africa. Enhanced diagnoses of *Cynelos* and *Amphicyon* also permit the reallocation of some other previously described specimens to these taxa. These include: assignment of "*Amphicyon* sp." and an isolated m2 previously identified as "*Afrocyon burolleti* Arambourg, 1961" from Gebel Zelten, Libya, to the new species of *Cynelos*; allocation of "*Ysengrinia*" *ginsburgi* from Arrisdrift, South Africa, to *Cynelos ginsburgi* n. comb.; and attribution of a giant undescribed additional species from Buluk, Kenya to *Cynelos* sp. Other specific specimens from Gebel Zelten and Kenya, currently assigned to *Afrocyon*, are also transferred to either *Cynelos* or *Amphicyon*. Results from this study, combined with previous work on the Moghra carnivores, suggests that at least three and perhaps as many as four very large carnivorous genera co-existed at Moghra: *Cynelos*, *Amphicyon*, *Hyainailouros* Stehlin, 1907 and possibly *Megistotherium* Savage, 1973. These giants represent the top predators of the Early Miocene of Africa, with *Cynelos* being more carnivorous, and *Amphicyon*, *Hyainailouros* and *Megistotherium* having more developed bone-crushing capabilities.

KEY WORDS
Cynelos,
Amphicyon,
Afrocyon,
Paleobiogeography,
Immigration events,
new combination,
new species.

RÉSUMÉ

Nouveaux amphicyonidés (Mammalia, Carnivora) du Miocène inférieur de Moghra, Égypte.
Nous décrivons ici deux mandibules de grands amphicyonidés (Amphicyonidae, Carnivora) de Moghra, Miocène inférieur, Égypte. L'une appartient à une nouvelle espèce de *Cynelos* Jourdan, 1862 de la même taille que *C. macrodon* (Savage, 1965) et *C. ginsburgi* n. comb., mais dont la lame du paraconide est relativement plus longue. L'autre est attribuée à *Amphicyon giganteus* (Schinz, 1825). À partir de ce nouveau matériel, les différences entre *Cynelos*, *Amphicyon* Lartet in Michelin, 1836 et *Afrocyon* Arambourg, 1961 sont clarifiées. De là nous déterminons trois (P4, M1, M2) sur quatre dents d'amphicyonidés isolées et non associées de Moghra, précédemment attribuées à « *Cynelos* sp. nov. » à *Amphicyon giganteus*. Cela représente la première signalisation de dents supérieures d'*A. giganteus* en Afrique. Les diagnoses remaniées de *Cynelos* et *Amphicyon* permettent également de ré-attribuer certains spécimens appartenant à ces taxons décrits précédemment. Cela permet d'attribuer «*Amphicyon* sp.» et une m2 isolée du Djebel Zelten en Libye identifiés comme «*Afrocyon burolleti* Arambourg, 1961» à la nouvelle espèce de *Cynelos*; l'attribution de « *Ysengrinia* » *ginsburgi* d'Arrisdrift, Afrique du Sud, à *Cynelos ginsburgi* et l'attribution d'une espèce géante additionnelle non décrite de Buluk, Kenya, à *Cynelos* sp. D'autres spécimens du Djebel Zelten et du Kénya, assignés actuellement à *Afrocyon*, sont aussi transférés à *Cynelos* ou *Amphicyon*. Les résultats de cette étude, combinés à un précédent travail sur les carnivores de Moghra, suggèrent qu'au moins trois, peut être quatre, genres de très grands carnivores coexistaient à Moghra ; *Cynelos*, *Amphicyon*, *Hyainailouros* Stehlin, 1907 et peut être *Megistotherium* Savage, 1973. Ces géants représentent le sommet des prédateurs du Miocène inférieur d'Afrique, *Cynelos* étant le plus carnivore et *Amphicyon*, *Hyainailouros* et *Megistotherium* possédant des capacités de broyeurs d'os plus marquées.

MOTS CLÉS
Cynelos,
Amphicyon,
Afrocyon,
Paléobiogéographie,
événement d'immigration,
combinaison nouvelle,
espèce nouvelle.

INTRODUCTION

Amphicyonidae is the most diverse extinct family of caniform Carnivora. Members of the group span a temporal range from the late Eocene (Tomiya & Tseng 2016) to the late Miocene, and a geographic breadth across sites in Africa, Eurasia, and North America. The dietary preferences among members of the Amphicyonidae are also correspondingly broad, ranging from omnivory, e.g., the bunodont *Pseudarctos* Schlosser, 1899 (Schlosser 1899, Nagel *et al.* 2009) to hypercarnivory, e.g., *Myacyon* Sudre & Hartenberger, 1992 or *Agnotherium* Kaup, 1833 (Morales *et al.* 2016). Some amphicyonids are also among the largest members of Carnivora ever known (Sorkin 2006; Figueirido *et al.* 2011).

In Africa, amphicyonids are present throughout the Miocene, although the large to very large taxa are best known from the Early Miocene, mostly corresponding to European MN 3-4. These are: 1) *Cynelos* (synonym of *Hecubides*) (Morlo *et al.* 2007; Werdelin & Peigné 2010; Leakey *et al.* 2011; Adrian *et al.* 2018); 2) *Amphicyon giganteus* (Schinz, 1825) (Morales *et al.* 2003); and 3) *Afrocyon burolleti* Arambourg, 1961 (Morales *et al.* 2010, 2016).

Morlo *et al.* (2007) referred four large isolated teeth from Moghra to *Cynelos* sp. nov. These specimens were later placed in "*Ysengrinia*" *ginsburgi* Morales, Pickford, Soria & Fraile (Morales *et al.* 2010) and subsequently discussed as representing either *Cynelos* sp. (Werdelin & Peigné 2010), "*Afrocyon* n. sp." (Morales *et al.* 2016) or *Cynelos macrodon* (Savage, 1965) (Adrian *et al.* 2018). Here we review the morphology of these specimens and demonstrate that they belong to two different taxa, *Cynelos* and *Amphicyon* Lartet in Michelin, 1836. We also describe two new additional mandibular specimens from Moghra, one of which represents a new species of *Cynelos*, and the other documents the first record of *Amphicyon* in Egypt. The description of this material helps clarify the differences among species of African *Cynelos*, as well as the relationship between *Cynelos* and the two other large Early Miocene amphicyonid genera from Africa, *Amphicyon* and *Afrocyon* Arambourg, 1961.

MATERIAL AND METHODS

Both amphicyonid mandibles were collected during the 2005 field season from the same stratigraphic horizon, but they are not associated with each other. The terminology and nomenclature of the tooth morphology is taken from Van Valen (1994) and Smith & Dodson (2003). The method of dental measurement follows Peigné & Heizmann (2003). Dental measurements were taken with calipers to the nearest 0.1 and are given in mm. Herein, length refers the greatest mesiodistal length of the tooth crown and width refers to the greatest labiolingual width of the tooth. The dimensions of the alveoli were measured if teeth were absent. In addition, the length and width (maximum) of the mandible and the height of the mandible behind each molar was measured if available (for measurements see Table 1). Comparative material is mentioned in the text.

ABBREVIATIONS

Anatomical abbreviations

P/p	upper/lower premolar;
M/m	upper/lower molar.

Institutional abbreviations

CUWM	Cairo University, Moghra collection, Cairo;
DPC	Duke University Primate Center, Division of Fossil Primates, Durham, North Carolina;
KNM	National Museums of Kenya, Nairobi;
MNCN	Museo Nacional de Ciencias Naturales, Madrid;
NMB	Naturkundemuseum Basel, Basel;
NHM	Natural History Museum, London;
NHMW	Naturhistorisches Museum, Wien;
PQAD	Field number for specimens from Arrisdrift (Morales *et al.* 1998).

GEOLOGICAL AND STRATIGRAPHIC SETTING

Moghra comprises a number of Early Miocene fossil localities occupying the northeastern portion of the Qattara Depression, approximately 60 km south of El Alamein, Egypt (Fig. 1). The Moghra Formation overlies the Dabaa Formation (subsurface), an Oligocene marine shale, and underlies the Marmarica Formation, a Middle Miocene marine limestone that forms the top of the Qattara escarpment. Recent geological work (Hassan 2013) indicates that in large scale the Moghra Formation represents a series of nine transgressive-regressive units, within which three smaller sub-unit lithofacies occur: 1) tidally influenced fluvial channel, estuary, and tidal channel/bar deposits; 2) shelf deposits; and 3) upward-coarsening deltaic deposits. In essence, the vertical architecture of the Moghra Formation represents a series of estuarine units stacked in a net transgressive stratigraphy. The vertebrate fauna has been reported in four stratigraphic horizons found on the basal part of units 2, 6, 8, and 10, and known as F1, F2, F3, and F4 respectively (AbdelGawad *et al.* 2010, 2012; AbdelGawad 2011). Each horizon represents an erosional lag surface; characterized by lag deposits and composed of mudclasts associated with coprolites and silicified wood. Miocene mammalian fossils come from the fluvial-tidal estuarine portions of the Moghra sequence (Hassan *et al.* 2012).

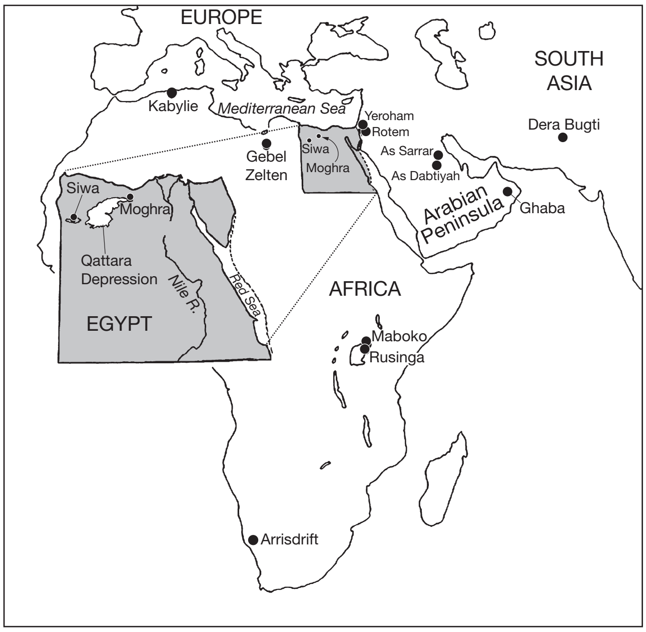


FIG. 1. — Location of Moghra, Egypt.

Due to the absence of volcanic deposits, the age of the Moghra fauna was estimated to be *c.* 18 Ma based on faunal correlation with sites in East Africa (Miller 1999, Morlo *et al.* 2007). In particular, the composition of the Moghra fauna most closely matched the assemblage from Rusinga Island, Kenya, which was dated to 17.8 +/- 0.2 (Drake *et al.* 1988). Recent re-dating of both the Rusinga and Moghra deposits refines but does not contradict the finding that the Moghra and Rusinga faunas are largely pene-contemporaneous. Recent work at Rusinga combining ^{40}Ar/^{39}Ar dating with paleomagnetism analyses indicates that the fossiliferous deposits were deposited between *c.* 20 and *c.* 17 Ma (Peppe *et al.* 2016, 2017). These analyses also reveal that the historical museum collection from the very rich Hiwegi Formation on Rusinga combines faunas from at least two different and temporally separate environments, suggesting that the bulk of the published Hiwegi collection represents a time-averaged assemblage (Peppe *et al.* 2016, 2017). At Moghra, results from 87Sr/86Sr dating have shown that the Moghra sequence ranges in age from 21 Ma near base of the section to 17 Ma at the top. The majority of the fossils are derived from the lower to middle part of the section, dated between 19.6-18.2 Ma, although as with the Rusinga collection, the Moghra museum assemblage represents a time-averaged sample, with some, although fewer, specimens derived from deposits approaching 17 Ma (Hassan 2013).

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821
Family Amphicyonidae Haeckel, 1866
Subfamily Amphicyoninae Trouessart, 1885

Genus *Cynelos* Jourdan, 1862

Type species. — *C. lemanensis* (Pomel, 1846), subsequent designation by Jourdan (1862).

Diagnosis. — Emended after Peigné & Heizmann (2003), Werdelin & Peigné (2010): small to large sized amphicyonids with low, slender mandibles; diastemata between anterior premolars; premolars widest distally; p4 with strong postprotocuspid; the p4 is larger in relation to m1 and to m2 than in *Amphicyon*, the tip of the main cusp of p4 does not project posteriorly, and the p4 talonid is wider; m1 with low metaconid and tall hypoconid crest, entoconid crest distinct but low, talonid wider than trigonid; m2 mesiodistal length about two thirds the length of m1, m2 lacking the paraconid, with a long and wide talonid, protoconid lacking a distal crest; m3 single-rooted and not double rooted as in *Afrocyon*, P4 with small protocone, M1 rectangular, M2 slightly more reduced than M1, with paracone slightly larger than metacone, and v-shaped hypocone crests in African specimens.

Referred African species. — *Cynelos anubisi* n. sp., from Moghra (includes "*Amphicyon* sp." in Morales *et al.* 2010: fig. 4), *Cynelos euryodon* (Savage, 1965), *Cynelos ginsburgi* (Morales, Pickford, Soria & Fraile, 1998) n. comb., *Cynelos macrodon* (Savage, 1965), *Cynelos minor* (Morales & Pickford, 2008), *Cynelos* sp. from Buluk, Kenya (KM WS 12663, Anemone *et al.* 2005).

Remarks

Cynelos is a widespread genus of amphicyonid carnivoran known from the late Oligocene through Early Miocene of Africa (Hooijer 1963; Werdelin & Peigné 2010) and Europe (Peigné & Heizmann 2003), Early to Middle Miocene of North America (Hunt 1998; Hunt & Stepleton 2015), and the Middle Miocene of Asia (Jiangzuo *et al.* 2018). North American and European members are well known (e.g., Viranta 1996; Hunt 1998; Peigné & Heizmann 2003; Hunt & Stepleton 2015), and the Asian material was recently reviewed (Jiangzuo *et al.* 2018). Individual species representing the African record of the genus have been discussed by several authors (e.g., Morales & Pickford 2005, 2008; Morlo *et al.* 2007; Morales *et al.* 1998, 2003, 2008, 2010; Adrian *et al.* 2018), with overviews given in Werdelin & Peigné (2010) and Morales *et al.* (2016).

Savage (1965) described two amphicyonids, a small species, *Hecubides euryodon* Savage, 1965 from Napak-I in Uganda, and a large one, *Hecubides macrodon* Savage, 1965, from Rusinga Island, Kenya. *Hecubides* Savage, 1965 was later included in *Cynelos* (Ginsburg 1980), a decision followed by nearly all researchers (e.g., Schmidt-Kittler 1987; Morales *et al.* 1998; Pickford *et al.* 2003; Peigné & Heizmann 2003; Peigné *et al.* 2006a, b; Morlo *et al.* 2007; Werdelin & Simpson 2009; Werdelin & Peigné 2010; Leakey *et al.* 2011; Hunt & Stepleton 2015; Jiangzuo *et al.* 2018; Adrian *et al.* 2018). One exception to this is the work of Morales and colleagues (Morales & Pickford 2005; Morales *et al.* 2007, 2008, 2010, 2016), who emphasized differences between *H. euryodon* and the type species of *Cynelos*, *C. lemanensis* (Morales *et al.* 2016). However, as Jiangzuo *et al.* (2018) discussed, the features cited in favor of retaining the name *Hecubides* (Morales *et al.* 2016) can be regarded as intrageneric if other species of *Cynelos* are considered. Here we follow the majority of authors in recognizing *Hecubides* as a junior synonym of *Cynelos.*

Despite acknowledging the close morphological relationship between "*Hecubides*", *Cynelos macrodon*, and "*Cynelos* sp. nov." from Moghra (Morlo *et al.* 2007), Morales *et al.* (2016) moved these large *Cynelos* species from the genus *Hecubides/Cynelos* to *Afrocyon*, a monotypic taxon erected on the basis of a partial mandible from the Early Miocene of Gebel Zelten in Libya (Arambourg 1961). This assignment effectively promoted the view that *Cynelos* was a taxon restricted to northern continents, and that all Early Miocene African amphicyonids belong to either the small *Hecubides* or the large *Afrocyon*, with the exception of *Amphicyon giganteus* from Arrisdrift, Namibia. Recently, Adrian *et al.* (2018) described new Early Miocene material from Kalodirr, Kenya, and attributed it to *C. macrodon*, although without mentioning the previous allocation of *Cynelos* to the North African taxon *Afrocyon*. Here we follow Adrian *et al.* (2018) and discuss clear differences between *Cynelos* and *Afrocyon*, which unite *C. macrodon* with *C. lemanensis*, *C. euryodon* and other African specimens. Consequently, we not only re-establish the occurrence of *Cynelos* in Africa, but also recognize six African species in the genus: small *C. euryodon* and *C. minor*, large *C. macrodon*, *C. ginsburgi* n. comb., *Cynelos anubisi* n. sp. from Moghra, and a very large species from Buluk, Kenya.

Cynelos anubisi n. sp.
(Fig. 2)

urn:lsid:zoobank.org:act:EED887B0-9F1C-4ADD-B4CF-7E8BBEB7514D

Cynelos sp. nov. – Morlo *et al.* 2007: fig. 4G, H.

cf. *Ysengrinia ginsburgi* – Morales *et al.* 2010: 48.

Afrocyon burolleti – Morales *et al.* 2010: fig. 3.

Amphicyon sp. – Morales *et al.* 2010: fig. 4.

Cynelos sp. – Werdelin & Peigné 2010: 604.

Afrocyon n. sp. – Morales *et al.* 2016: 143.

Holotype. — CUWM 55, left mandible with alveolus of c, single root of p1, single root of p2, roots of p3, p4-m2, and alveolus of m3.

Paratype. — DPC 14532/2 L-7, isolated left m1 from Moghra, Egypt (Morlo *et al.* 2007: fig. 4G, H).

Referred material. — MNCN 79042 right mandible fragment with alveolus of p1, single-rooted p2, fragment of p3, and p4 from Gebel Zelten, Libya (= BIZ.2A.15 in Morales *et al.* 2010: fig. 4). NHM M 82374, an isolated left m2 from Gebel Zelten, Libya (Morales *et al.* 2010: fig. 3).

TABLE 1. — Specimen measurements. Data from literature: **a**, Morlo *et al.* (2007); **b**, Morales *et al.* (2010); **c**, Morales *et al.* (2016); **d**, Adrian *et al.* (2018); **e**, Morales *et al.* (2003); **f**, Morales *et al.* (1998); **g**, Bastl *et al.* (2018).

Taxon	**Specimen**	**Locality**	**Skeletal element**	**Length**	**Breadth**
Cynelos anubisi n. sp.	CUMW 55	Moghra	alveolus of p1	3.8	3.6
			diastema length p1-p2	4.6	–
			alveolus of p2	4.4	4.3
			diastema length p2-p3	12.2	–
			alveoli of p3	14.3	6.3
			p4	18.0	10.0
			m1	28.9	14.3
			m2	21.0	14.5
			alveolus of m3	11.4	8.0
			height of mandible beyond m1	54.0	
	DPC 14532/2 L-7[a]		m1	26.1	11.6
	MNCN 79042[b]	Gebel Zelten	p2	8.2	5.4
			p3	10.8	6.0
			p4	17.3	8.7
	NHM M 82374[b]	Gebel Zelten	m2	17.9	13.2
Cynelos macrodon	NHM M 34303[c]	Rusinga	m1	25.8	11.6
	KNM-WK16984[d]	Kalodirr	p4	21.1	11.6
Cynelos cf. *macrodon*	KNM-MY 89	Rusinga	m2	20.5	12.9
Cynelos ginsburgi n. comb.	AD 242'99[e]	Arrisdrift	p4	15.4	8.4
	AD 311'97[e]		m1	29.0	13.9
	PQAD 133[e]		p4	14.5	8.0
			m1	27.2	12.0
			m2	17.0	11.5
			m3	10.6	8.0
Amphicyon giganteus	CUMW 53	Moghra	alveolus of p1	10.0	6.4
			fragmental p2	15.0	7.9
			alveoli of p3	20.0	11.4
			alveoli of p4	25.5	12.9
			m1	38.4	19.7
			m2	28.5	20.3
	DPC 14532/1[a]	Moghra	P4	29.6	17.5
	DPC 5426[a]	Moghra	M1	21.7	24.5
	DPC 8981[a]	Moghra	M2	17.8	25.7
	NHM M 82373[b]	Gebel Zelten	p4	(15.7)	9.1
			m1	28.2	13.2
			m2	19.3	13.2
	PQAD 1520[f]	Arrisdrift	p4	21.3	14.3
			m1	35.5	19.0
			m2	26.5	21.5
	NHMW 2015/0009/0001a[g]	Gracanica	p4	16.2	11.0
	NHMW 2015/0009/0001b[g]		m1	36.1	19.3
	NHMW 2015/0009/0001c[g]		m2	24.2	17.5
	NMB S.O.6531[g]	Chilleurs-aux-bois	p4	18.4	10.0
			m1	33.3	17.3
			m2	24.4	20.4
Afrocyon burolleti	MNHN 1961-5-7[b]	Gebel Zelten	p4	19.8	11.2
			m1	31.0	15.3
			m2	23.3	13.9

TYPE LOCALITY. — Wadi Moghra, Egypt.

DISTRIBUTION. — North Africa: Egypt and Libya.

AGE AND HORIZON. — Late Early Miocene, contemporaneous with European biozone MN4.

ETYMOLOGY. — "*anubisi*" after "Anubis", the Greek name for the Ancient Egyptian jackal-headed god, who watched over the dead.

DIFFERENTIAL DIAGNOSIS. — *Cynelos anubisi* n. sp. differs from *Amphicyon* and *Afrocyon* in having a single-rooted p1 and p2, a long diastema between p2 and p3, and a short diastema between p3 and p4. The m1 metaconid of *C. anubisi* n. sp. is more reduced, the hypoconid is smaller, and the m1 and m2 talonids are narrower. The m2 protoconid and hypoconid are low but massive. *Cynelos anubisi* n. sp. further differs from *Amphicyon* in having a narrower m2, as a result of an elongated talonid. All molars lack cingulids. Further differs from *Afrocyon* in having a single-rooted m3, and a coronoid process that rises at a shallower angle. *Cynelos anubisi* n. sp. is about the same size as, or is slightly smaller than *C. macrodon*, but *C. anubisi* n. sp. differs from *C. euryodon* and *C. minor* in being much larger in size, and differs from the Buluk *Cynelos* in being much smaller. *Cynelos anubisi* n. sp. differs from *C. euryodon* and *C. lemanensis* in having a single rather than a double rooted p2, and a much shorter p3-p4 diastema (see Peigné & Heizmann 2003; Morales *et al.* 2016); differs from *C. macrodon* and *C. ginsburgi* n. comb. in having m1 with a longer paraconid blade relative to overall tooth size; further differs from *C. macrodon* in having the m1 paraconid oriented slightly more anteriorly, having

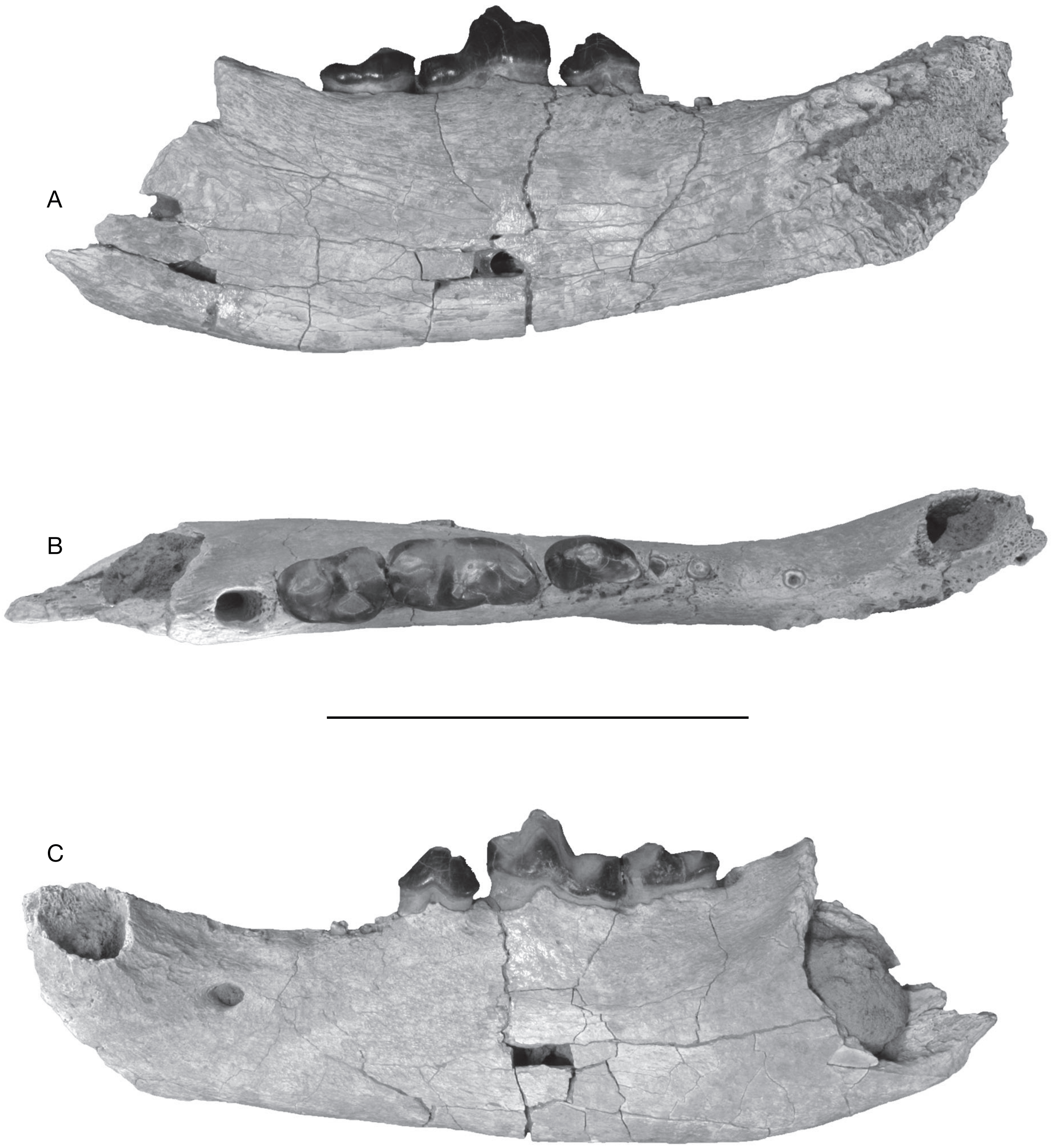


Fig. 2. — CUWM 55, Moghra, Early Miocene. Holotype of *Cynelos anubisi* n. sp.: **A**, lingual view; **B**, occlusal view; **C**, labial view. Scale bar: 100 mm.

p4 smaller, and in possessing small p4 pre- and postprotoconulids; and further differs from *C. ginsburgi* n. comb. in having p4 and m2 longer relative to m1, m1 broader the m1 paraconid less angled but relatively longer, and the metaconid is located slightly more anteriorly. *Cynelos anubisi* n. sp. is larger than any Eurasian *Cynelos* species, including *C. bohemicus* (Schlosser, 1899) which is known from Europe and Asia during biozones MN 3 to MN 5 (Jiangzuo *et al.* 2018). *Cynelos anubisi* n. sp. also clearly differs from *C. bohemicus* in possessing a large diastema between p2 and p3 that is absent in this Eurasian species (see Fejfar & Heizmann 2016: fig. 9.5). Additionally, the generic assignment of material representing *C. bohemicus* is controversial. Schlosser (1899) originally placed the taxon in the genus *Pseudocyon*, although more recent contributions have discussed the material as belonging to *Amphicyon* (Fejfar & Heizmann 2016, following Kuss 1965) or *Cynelos* (Jiangzuo *et al.* 2018, following Hunt 1998; Hunt & Stepleton 2015).

Descriptions and comparisons

In the holotype mandible, CUWM 55, p4, m1, and m2 are present, while the canine, p1-p3, and m3 are represented by alveoli. Judging from the alveoli, *C. anubisi* n. sp. had a single-rooted p1 and p2, and a small, double rooted p3, with a long diastema between p1-p2, longer than that observed in MNCN 79042 from Gebel Zelten. An alternative possible interpretation is that p1 in *C. anubisi* n. sp. is reduced, and the p2 is double-rooted, but this is not the condition observed in MNCN 79042. In this respect, *C. anubisi* n. sp. clearly differs from the other Moghra amphicyonid CUWM 53, the Gebel Zelten specimen NHM M 82373, *Amphicyon giganteus* from Arrisdrift (Morales *et al.* 2003), and *Afrocyon burolleti*

(Morales *et al.* 2010), all of which have a double-rooted p2 and lack diastemata in the premolar series.

The p4 is a typical amphicyonid tooth with the posterior part being broader than the anterior. The tooth is smaller than that of *Cynelos macrodon* from Kenya (Adrian *et al.* 2018), and is similar in size to that of MNCN 79042 from Gebel Zelten, although the p4 of *C. anubisi* n. sp. is slightly broader. A very low preprotoconulid is indicated by abrasion marks, a feature also present in the Gebel Zelten specimen. The protoconid is the tallest cusp, forms the most voluminous part of the tooth, and also shows strong horizontal abrasion. A strong protoconulid about half the height of the protoconid was present on the distal margin of the tooth, but the protoconulid is abraded in this specimen. A small postprotoconulid is present on the distal end of the postprotocristid, and this feature lacks abrasion marks. Such a postprotoconulid is also present, although smaller, in MNCN 79042. This is in contrast to *C. ginsburgi* n. comb., where the p4 is relatively shorter compared to m1, with pre- and postprotoconulids present, and *C. macrodon*, which lacks both a preprotoconulid and postprotoconulid.

The morphology of m1 is preserved in the holotype and is also visible in DPC 14532 (Morlo *et al.* 2007). Both specimens are rather slender, with a low metaconid placed slightly distolingual to the protoconid. Both, the m1 of the type specimen, as well as of DPC 14532, are weathered and abraded, so the original heights of the paraconid, protoconid, and hypoconid are unknown. The lingual border of the talonid is occupied by a small hypoconulid and an even smaller entoconid. The m1 of *C. anubisi* n. sp. is about the same size as in *C. macrodon*, but *C. anubisi* n. sp. has a relatively longer paraconid blade, even longer than that observed for *C. ginsburgi* n. comb. However, *C. anubisi* n. sp. and *C. macrodon* share a more angled paraconid blade than *C. ginsburgi* n. comb., as well as a metaconid that is positioned slightly more anteriorly. The apex of the m1 metaconid in *C. ginsburgi* n. comb. is tilted slightly distally, but due to abrasion this feature cannot be determined for the m1 of *C. macrodon* and *C. anubisi* n. sp.

The m2 in *C. anubisi* n. sp. is a massive, elongated tooth in which the protoconid is larger than the metaconid, and the hypoconid approaches the size of the protoconid. Although the tooth is worn and abraded, the original height of the three cusps would have been low. A small entoconid is present on the lingual margin of the tooth. In contrast to *Amphicyon*, the talonid basin is greatly reduced. As in p4 and m1, there is no development of a cingulid. The very same features are present in an isolated m2 NHM M 82374, assigned to *Afrocyon burolleti* by Morales *et al.* (2010: fig. 3) from Gebel Zelten, although the Libyan tooth differs from CUWM 55 in being about 15% smaller. Both the Moghra and Gebel Zelten m2s differ from the holotype of *Afrocyon burolleti* in being proportionally broader, with a length/breadth ratio of 1.4, while this same figure is about 1.7 in *Afrocyon*.

The m3 is represented only by its alveolus, although the depth and conical shape of the feature suggests a small but substantial tooth, which would have participated in the grinding function of the molar row. It differs from m3 of *Afrocyon* in being single-rooted.

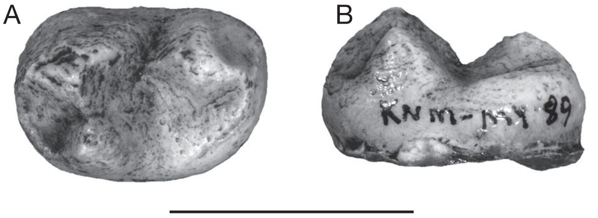


Fig. 3. — KNM-MY 89, isolated left m2 from the Muruyur Formation, Kenya, Middle Miocene, *Cynelos* cf. *macrodon*: **A**, labial view; **B**, occlusal view. Scale bar: 20 mm.

The mandibular symphysis in *C. anubisi* n. sp. extends slightly more posteriorly, past p2, as compared with MNCN 79042 from Gebel Zelten, in which the symphysis ends directly below p2. In addition, the *C. anubisi* n. sp. mandible has two mental foramina, one located between p1 and p2, and the other situated slightly posterior to p4. In MNCN 79042 the anterior mental foramen is located slightly more anteriorly below p2, and two smaller foramina are present beyond the anterior root of p4.

REMARKS

All African members of the genus *Cynelos* are united by the presence of diastemata between reduced premolars, a feature that distinguishes *Cynelos* from the other Early Miocene African amphicyonids, *Amphicyon* and *Afrocyon*. The occurrence of a diastema between p2 and p3, and the overall trenchant tooth morphology are features shared among *Cynelos* from Moghra, the type species of *Cynelos* (the European *C. lemanensis*), and African *C. euryodon*.

Based on the mandible CUWM 55 we erect a new species of *Cynelos*, *C. anubisi* n. sp. The m1, DPC 14532/2 (Morlo *et al.* 2007) described previously is designed as the paratype. Additionally, a mandibular fragment from Gebel Zelten, MNCN 79042, previously discussed as "*Amphicyon* sp." (Morales *et al.* 2010), is also assigned to *C. anubisi* n. sp., due to a shared similarity in size, a shared low and slender morphology of the mandibular ramus, and the combined presence of a single rooted p1 and p2, a long diastema between p2 and p3, a very short diastema between p3 and p4, the occurrence of pre- and postprotoconulids on p4, and lack of cingulids. In addition, an isolated m2 NHM M 82374 from Gebel Zelten is provisionally referred to *C. anubisi* n. sp. due to its rectangular outline and small mesiolingual enlargement, which differ both from *Afrocyon*, and from the m2 in the mandible NHM M 82373 (Morales *et al.* 2010: fig. 2) currently attributed to cf. *Amphicyon* (see below). We thus assign the tooth to *Cynelos anubisi* n. sp., while recognizing that the Gebel Zelten specimen is slightly smaller than the m2 of the holotype.

Cynelos anubisi n. sp. differs from similar sized *Cynelos* in having a longer paraconid blade. However, a thorough comparison between *C. anubisi* n. sp. and *C. macrodon* is hampered by the fact that the only teeth available for comparison are p4 and m1. Indeed, among species of *Cynelos*, *C. macrodon* is not very well represented. The holotype of *C. macrodon* is an M1 from Rusinga Island, Kenya (Savage 1965), and the hypodigm is comprised of only isolated teeth. These include m1 and M1 fragments (Schmidt-Kittler 1987), an additional m1 (Morales *et al.* 2016), recent material from Kalodirr, which is a p4, P4, and M1 (Adrian *et al.* 2018), and an M2 from Napak-I, assigned to "*Afrocyon* sp." by Morales *et al.* (2016: figs. 2, 6). Pickford *et al.* (2003) identified "?*Cynelos*" as present in the fauna from Moroto, Uganda, and Leakey *et al.* (2011) list a few records of *C. macrodon* from sites in the Turkana Basin. However, except for the material discussed by Adrian *et al.* (2018), descriptions of *C. macrodon* are generally lacking. While the m1 of *C. macrodon* from Rusinga (Schmidt-Kittler 1987, Morales *et al.* 2016) is about the same size as the m1 of *C. anubisi* n. sp., the Rusinga specimen lacks the long paraconid blade and shorter protoconid of *C. anubisi* n. sp. Compared with *C. macrodon* from Kalodirr (Adrian *et al.* 2018), the p4 of *C. anubisi* n. sp. is smaller and possesses pre- and postprotoconulids. We consider possession of a longer m1 paraconid blade to be an important character distinguishing *C. anubisi* n. sp. from *C. macrodon.* Confidence in this feature as a diagnostic character is based on the observation that, among species of *Cynelos*, members of *C. euryodon* exhibit variation in a number of ways, including the height of the m1 hypoconid, the size of the antero-labial enlargement, cusp height, and strength of the anterior cingulid in m2, but not in the length of the m1 paraconid blade (pers. obs. MM on KNM without number, KNM RU 2986, KNM RU 4393).

Finally, a lower canine and M2 from the Middle Miocene Muruyur Formation, Kenya, were attributed to *C. macrodon* by Morales & Pickford (2008), but were subsequently transferred to *Myacyon* by Morales *et al.* (2016). The specimen KNM-MY 89 (Fig. 3) is a left m2 from the same area. This tooth is part of the carnivoran collection described by Schmidt-Kittler (1987), but this particular specimen was not included in his monograph because it was misplaced at the time. The morphology of KNM-MY 89 is much closer to *Cynelos* than to *Myacyon* (see Morales *et al.* 2010: fig. 3, 6) because it is nearly identical to the m2 of CUWM 55 and to NHM M 82374 from Gebel Zelten. Due to this morphological resemblance we refer the lower canine, M2, and m2 from the Muruyur Formation to *Cynelos* cf. *macrodon*, thereby re-instating the initial view of Morales & Pickford (2008). These specimens represent the only record of a large middle Miocene *Cynelos* in Africa.

Morales *et al.* (2010) referred the Moghra specimens described by Morlo *et al.* (2007) as "*Cynelos* sp. nov." to the species "*Ysengrinia*" *ginsburgi* from Arrisdrift (Morales *et al.* 1998: fig. 4; Morales *et al.* 2003; Werdelin & Peigné 2010). Due to the presence of a large M2, Morales *et al.* (2016) excluded the taxon from *Ysengrinia* and transferred it to *Afrocyon*. However, the Arrisdrift species differs from *Afrocyon burolleti* and resembles *C. anubisi* n. sp. in possessing a much more trenchant dentition with narrower m1 and m2 talonids, and in having a diastema between p2 and p3 (Morales *et al.* 1998, 2003). We thus corroborate the exclusion of the species from *Ysengrinia*, but transfer it from *Afrocyon* to *Cynelos* as *C. ginsburgi* n. comb. *Cynelos anubisi* n. sp. and *C. macrodon* differ from *C. ginsburgi* n. comb. in having the m1 metaconid located slightly more anteriorly, and *C. anubisi* n. sp. further differs from *C. ginsburgi* n. comb. in having p4 and m2 larger relative to m1. *Cynelos ginsburgi* n. comb. differs from *C. macrodon* in having the P4 protocone less reduced, M1 less triangular, and pre- and postprotoconulids present on p4 (see Morales *et al.* 1998). *Cynelos ginsburgi* n. comb. also has a shortened M1 talon (see Adrian *et al.* 2018 for *C. macrodon* and Morales *et al.* 2016 for *C. ginsburgi* n. comb.) relative to *C. macrodon*, but this abbreviated talon occurs to a much lesser degree in *C. ginsburgi* n. comb. than it does in *Amphicyon giganteus* from Moghra.

Genus *Amphicyon* Lartet *in* Michelin, 1836
(see Peigné 2012)

Amphicyon giganteus (Schinz, 1825)
(Fig. 4)

In the synonym list, only first description and citations of the African record is given.

Canis giganteus Schinz, 1825: 342.

Canis d'une taille gigantesque – Cuvier 1824: pl. 193, fig. 20.

Amphicyon giganteus – Kuss 1965: 66. — Morales *et al.* 1998: fig. 7; 2003: 180. — Jiangzuo *et al.* 2019: 6.

Amphicyonidae gen. et sp. indet. – Hendey 1978: fig. 4.

Megamphicyon giganteus – Morales *et al.* 2016: 147.

HOLOTYPE. — M7753, Muséum d'Orléans, France.

TYPE LOCALITY. — Avaray, France.

AGE AND HORIZON IN AFRICA. — Late Early Miocene, contemporary to European biozone MN4.

AFRICAN RECORD. — Left P4 (DPC 14532/1), left M1 (DPC 5426), Left M2 (DPC 8981) from Egypt (Morlo *et al.* 2007), PQAD 1520, right mandible fragment from Arrisdrift, Namibia (Morales *et al.* 1998, 2003, 2016).

NEW SPECIMEN. — CUWM 53, left mandible fragment with crowns of m1-2, and alveoli for a single-rooted p1, double-rooted p2-p4, and a single-rooted m3.

DESCRIPTION AND COMPARISONS

The left mandible fragment CUWM 53 preserves the crown of m1, part of m2, and alveoli for a single-rooted p1, double-rooted p2-p4, and a single-rooted m3. No diastemata are present. As the inferior part of the mandible is broken, it is not possible to assess its original height.

Both m1 and m2 are robust teeth, including their roots. The m1 paraconid-protoconid blade appears to show strong wear, but this feature may be due in part to abrasion of this specimen. The protoconid is the tallest cusp of the trigonid, with the metaconid and paraconid subequal in height. The metaconid is tilted slightly posteriorly. The talonid makes up more than half of the tooth and a large hypoconid, which approaches the metaconid and paraconid in height, is present.

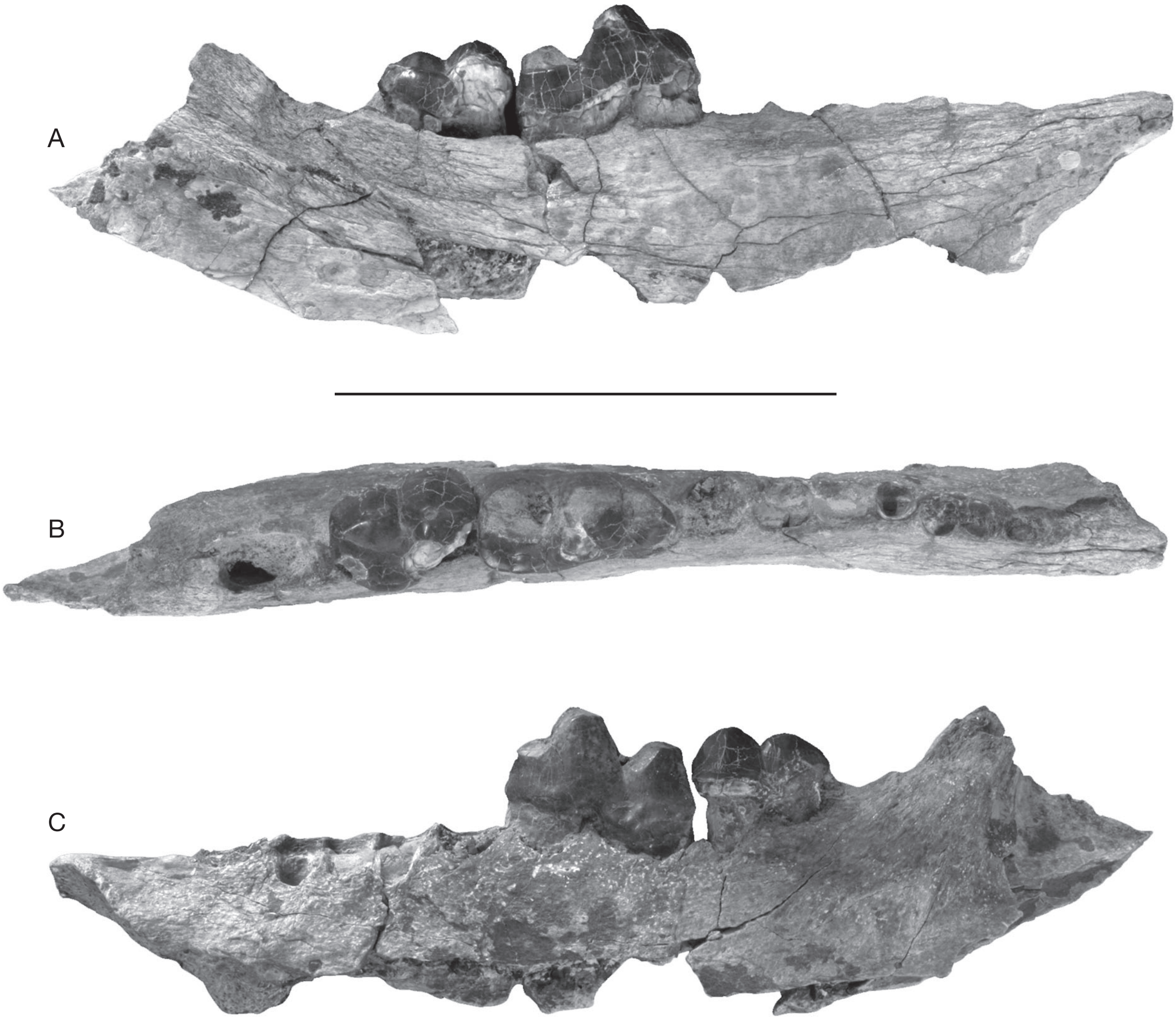


Fig. 4. — CUWM 53, Moghra, Early Miocene, *Amphicyon giganteus* (Schinz, 1825): **A**, lingual view; **B**, occlusal view; **C**, labial view. Scale bar: 100 mm.

The talonid also has a small entoconid, and a cingulid is present. The m2 is broken mesiolingually but a tall protoconid and lower metaconid are preserved. A crest extends from the metaconid distolingually to join the cingulid around the talonid.

Specimen CUWM 53 resembles *Amphicyon giganteus* and is assigned to that species rather than *Afrocyon* (Arambourg 1961) on the combined basis of having more slender m1 and m2, presence of a massive m1 talonid with the hypoconid as the most prominent cusp, an m2 which is subequal in height to the m1 talonid, lack of a talonid basin on m1, and the presence of an m3 alveolus indicating a single-rooted m3.

The Moghra mandible also shares a suite of features with *Amphicyon giganteus* from Arrisdrift (Hendey 1978; Morales *et al.* 1998, 2003). These include comparable size, a double-rooted p2, lack of premolar diastemata, m1 with a low metaconid and well-developed hypoconid, the presence of a paraconid on m2, and presence of a single-rooted m3. Morales *et al.* (2016) referred *Amphicyon giganteus* from Arrisdrift to the genus "*Megamphicyon*", a reassignment of the species suggested by the work of Kuss (1965), but a move that has been rejected by many authors (e.g., Ginsburg & Telles-Antunes 1968;Viranta 1996; Morales *et al.* 1998, 2003; Peigné *et al.* 2006a, 2008; Jiangzuo *et al.* 2018, 2019; Bastl *et al.* 2018). Here we join the majority and so recognize the species *A. giganteus* for the Arrisdrift and Moghra material.

European *A. giganteus* differs from *A. major* (Middle Miocene of Europe) in being larger on average, lacking diastemata between its premolars, having p4 larger (see Morales *et al.* 2003), m1 with an entoconid that is narrower and tapers posteriorly, and m2 with a higher trigonid (Jiangzuo *et al.* 2018). All of these characters also separate the African record of *A. giganteus* from *A. major*.

ADDITIONAL SPECIMENS

Three isolated upper teeth (P4: DPC 14532/1, M1: DPC 5426, M2: DPC 8981) from Moghra previously described as belonging to "*Cynelos* sp. nov." (Morlo *et al.* 2007) are here provisionally attributed to *A. giganteus*. These same specimens have been discussed by other authors as perhaps belonging to *Ysengrinia ginsburgi* (Morales *et al.* 2010: 48), "*Afrocyon* n. sp." (Morales *et al.* 2016), or *Cynelos macrodon* (Adrian *et al.* 2018).

The P4 resembles that of *A. giganteus* from La Barranca and Arroyo de Val (Peigné *et al.* 2006b: pl. 2, fig. 1-2), but has the protocone placed slightly more anterior. It differs from *C. macrodon* and *C. ginsburgi* n. comb. in having a much larger protocone, a feature that is nearly absent in *C. macrodon* and is greatly reduced in *C. ginsburgi* n. comb.

The M1 resembles A. *giganteus* from Farinheira (Ginsburg & Antunes 1995: pl. 1 fig. 2) and La Barranca (Peigné *et al.* 2008: pl. 2, fig. 5), but the talon of the Moghra specimen is shorter and narrower. In the former respect the Moghra M1 is reminiscent of the M1 of *A. eppelsheimensis* from the Late Miocene of Anjou (Gagnaison *et al.* 2017: fig. 2b). However, the two species are clearly different in that the M1 of *A. eppelsheimensis* displays a triangular occlusal outline (Kuss 1965, Morlo pers. observ.). The M1 from Moghra differs from members of *Cynelos* in having a mesiodistally very short talon relative to the trigon, with the protocone and metacone higher, more pronounced cingulae, and a small metaconule present. In these characters the Moghra specimen is unlike the holotype of *C. macrodon* from Rusinga (see Morales *et al.* 2016: fig. 9, 2A), and is even more distant from the *C. macrodon* material from Kalodirr described by Adrian *et al.* (2018: fig. 5.2-4). The short talon also distinguishes DPC 5426 from *C. ginsburgi* n. comb. (Morales *et al.* 2016: fig. 9, 5), *C. euryodon*, and *C. lemanensis*.

As with P4 and M1, the isolated M2 DPC 8981 from Moghra resembles European specimens of *A. giganteus*, in this case from Bézian (Ginsburg & Bulot 1982: pl. 1, fig. 2), Olival de Suzana (Ginsburg & Antunes 1995: pl. 1, fig. 2), and La Barranca (Peigné *et al.* 2008: pl. 2, fig. 6). The Moghra specimen differs from the M2 in *C. euryodon* (Morales *et al.* 2016: fig. 2, 4), *C. lemanensis* (Peigné & Heizmann 2003), *C. macrodon* from Napak-I, and *C.* cf. *macrodon* from the Muruyur Formation, in having a more rectangular shape, possessing stronger labial and lingual cingulae, and with u-shaped, rather than v-shaped hypocone crests.

Another African specimen possibly belonging to *Amphicyon* is the left mandible NHM M 82373 from Gebel Zelten, Libya, which has been discussed elsewhere as representing *Afrocyon burolleti* (Morales *et al.* 2010: fig. 2). However, the Gebel Zelten mandible differs from the poorly preserved holotype of *Afrocyon burolleti* (Arambourg 1961; Morales *et al.* 2010: fig. 1; Werdelin & Peigné 2010: fig. 32.1) in possessing a single-rooted m3, and in having a shallower mandible and less acute coronoid angle. The mandible also differs from *Cynelos* in lacking premolar diastemata, having p4 shorter relative to m1 and m2, and a broader talonid in m1 and the m2 with a wider mesiolingual enlargement. In all these features, NHM M 82373 resembles *Amphicyon giganteus*, although given the Gebel Zelten specimen's much smaller size, we refer the mandible to "cf. *Amphicyon*".

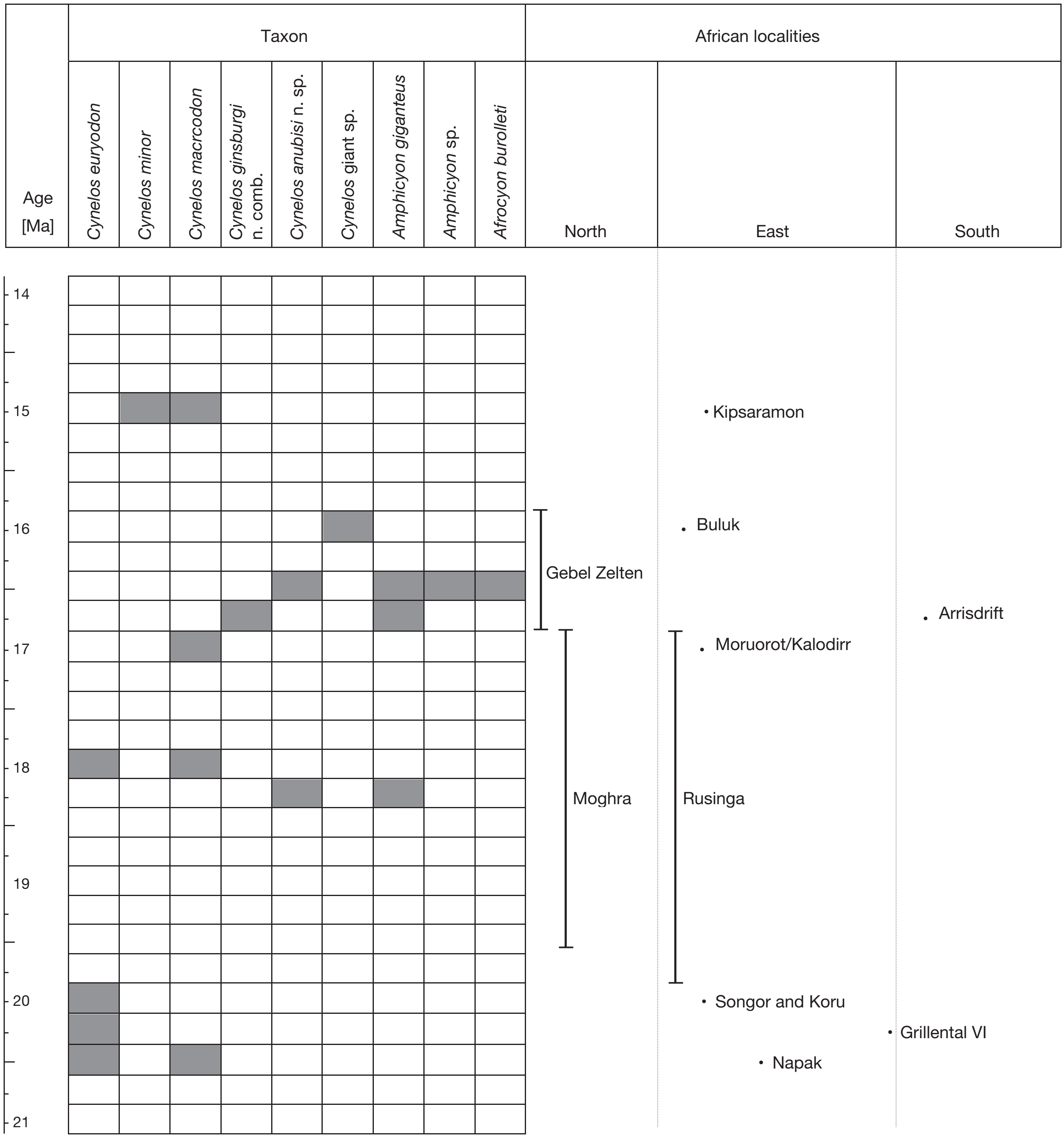
REMARKS

Fossil material of *Amphicyon giganteus* has been known since the time of Cuvier (1824), but the range of morphological variation within the species remains an open discussion. Until now, *A. giganteus* was represented in Africa only by the single mandible reported from Arrisdrift, South Africa (Morales *et al.* 1998) and some postcranial remains from Gebel Zelten, attributed to the species by Ginsburg (1980) and Ginsburg & Welcomme (2002). With the addition of CUWM 53 from Moghra, the species is again interpreted as having a pan-African distribution (Werdelin & Peigné 2010). The three isolated upper teeth from Moghra here attributed to *A. giganteus* are the first upper teeth described from *A. giganteus* in Africa. Even though there is little appropriate material available for comparison, the three specimens show features that are similar to those seen in *A. giganteus* from Europe (Ginsburg & Bulot 1982; Ginsburg & Antunes 1995; Peigné *et al.* 2008) and which have not been documented in *Cynelos,* namely: P4 has a much stronger protocone, M1 has an extremely short talon, and M2 has a peculiar morphology with u-shaped hypocone crests and an enlarged lingual cingulum. Re-evaluation of the mandible NHM M 82373 from Gebel Zelten suggests that a second, smaller species of *Amphicyon*, cf. *Amphicyon*, is also present in Africa. The Gebel Zelten mandible resembles the Moghra material of *A. giganteus* much more than it does to specimens of *Afrocyon burolleti* or *Cynelos.* However, NHM M 82373 is much smaller than *A. giganteus* and its m2 shows a slight mesiolingual enlargement not observed among other published *A. giganteus* specimens. *Amphicyon* has already been reported from Gebel Zelten based on postcranial material (Ginsburg 1980; Ginsburg & Welcomme 2002) that, however, is too large to belong to the same species as NHM M 82373. Large *Amphicyon* survived in Africa longer than on any other continent as is evidenced by "Amphicyonidae species A" from Lothagam (Werdelin 2003; Werdelin & Peigné 2010).

DISCUSSION

Recovery of new amphicyonid material from Moghra, combined with the re-analysis of specimens already described from Moghra and from elsewhere in Africa, makes clear that representatives of both *Cynelos* and *Amphicyon* were widespread across the continent during the Early Miocene. In contrast, *Afrocyon* is known only from the holotype mandible of *A. burolleti* recovered from Gebel Zelten, Libya. *Afrocyon* clearly differs from *Cynelos* and *Amphicyon* in having a double-rooted m3, a coronoid process that rises at a steeper angle, and a deeper mandible. In these features *A. burolleti* bears some resemblance to phoberocyonine and hemicyonine ursids, and although *Afrocyon* is larger than any species of *Phoberogale*, the ratio of p4 to m1 length appears similar to members of that Oligocene genus (see de Bonis 2013: table 4). *Afrocyon* is about the same size as *Phoberocyon*, but members of this taxon display a distinctive m2 paraconid and have a premasseteric fossa (see Wang *et al.* 2009), both absent in *Afrocyon*. In addition, the only record of an ursid in the Early Miocene of Africa is an isolated P4 from Rusinga (Schmidt-Kittler 1987). Werdelin & Peigné (2010) briefly discussed the specimen and regard it as a phoberocyonine rather than a hemicyonine. As this specimen cannot be directly compared to *Afrocyon* and clearly belongs to a much smaller animal, at present we choose to retain *Afrocyon* in Amphicyonidae.

TABLE 2. — Geographic and temporal distribution of *Cynelos* Jourdan, 1862, *Amphicyon* Lartet in Michelin, 1836, and *Afrocyon* Arambourg, 1961 in the Early and Middle Miocene of Africa. References: **Arrisdrift**, Morales *et al.* (2003); **Buluk**, Deino *et al.* (pers. comm.); **Grillental VI**, Morales *et al.* (2016); **Kipsaramon**, Behrensmeyer *et al.* (2002), Morales & Pickford (2008); **Koru and Songhor**: Morales & Pickford (2017), Wuthrich *et al.* (2019); **Moghra**, Hassan (2013); **Moruorot and Kalodirr**, Adrian *et al.* (2018), Deino *et al.* (pers. comm.); **Napak**, Gebo *et al.* (1997), Morales *et al.* (2016); **Rusinga**, Lukens *et al.* (2017), Peppe *et al.* (2011, 2016, 2017).



	Taxon									African localities		
Age [Ma]	*Cynelos euryodon*	*Cynelos minor*	*Cynelos macrcodon*	*Cynelos ginsburgi* n. comb.	*Cynelos anubisi* n. sp.	*Cynelos* giant sp.	*Amphicyon giganteus*	*Amphicyon* sp.	*Afrocyon burolleti*	North	East	South
14												
15		▨	▨								Kipsaramon	
16						▨					Buluk	
					▨		▨	▨	▨	Gebel Zelten		
				▨			▨					Arrisdrift
17			▨								Moruorot/Kalodirr	
18	▨		▨									
					▨		▨			Moghra	Rusinga	
19												
20	▨										Songor and Koru	
	▨											Grillental VI
	▨		▨								Napak	
21												

The generic differences between *Cynelos* and *Amphicyon* are clear irrespective of specimen size. African species of *Cynelos* are united with each other, and with the type species, *C. lemanensis* from Europe, in having diastemata between the premolars, much slenderer m1 and m2 talonids, a relatively longer m2, a reduced P4 protocone, and a relatively broader M1 talon (Peigné & Heizmann 2003). Features of the lower dentition that are available for comparison between *Cynelos* and *Afrocyon* confirm the generic separation of these two genera as well.

There is still much work to be done on the meaning of differences observed among *Cynelos* at the species level. A fairly large range of variation in size has been documented in the species *C. lemanensis* and *C. helbingi* (Peigné & Heizmann 2003, Hunt & Stepleton 2015). A number of researchers have noted the morphological variability present in the *C. euryodon* hypodigm (Morales *et al.* 2016; Jiangzuo *et al.* 2018), which includes size variation in the range of 10%, enlargement of the most mesial part of the m1 trigonid, height of the m1 hypoconid, and strength of the m2 anterior cingulid (includes MM pers. obs. on KNM without number, KNM RU 2986, KNM RU 4393).

While *C. ginsburgi* n. comb. and the giant *Cynelos* from Buluk are easily recognizable as separate species, *C. macrodon* and *C. anubisi* n. sp. may be interpreted as separate species, or as belonging to a single, temporally and spatially diverse species, *Cynelos macrodon*, which varies both in size and in morphological detail. We believe that distinguishing *C. anubisi* n. sp. from *C. macrodon* is appropriate because *C. anubisi* n. sp. displays pre- and postconulids on p4, and has a longer m1 paraconid, which are characters not known to vary even among specimens of *C. euryodon*.

Amphicyon differs from *Cynelos* mainly in having a more robust and less trenchant dentition, and in lacking premolar diastemata. Dental specimens of *Amphicyon* from Gebel Zelten (NHM M 82373) described here are not the first record of this taxon from Libya. Ginsburg (1980) and Ginsburg & Welcomme (2002) previously assigned a humerus and an astragalus from Gebel Zelten to *Amphicyon giganteus*, material that had originally been attributed to *Megistotherium* Savage, 1973 (Savage 1973). However, the attribution of dental material discussed here helps confirm the presence of *Amphicyon* in Libya, and together with records of *A. giganteus* from Moghra and Arrisdrift (Morales *et al.* 2003; Werdelin & Peigné 2010) the evidence suggests that, like *Cynelos*, members of *Amphicyon* also had a broad African distribution.

The presence of both *Cynelos* and *Amphicyon* at Moghra documented here, combined with previous work on the Moghra carnivores (Morlo *et al.* 2007), raises the number of very large genera known from the site to four: *Cynelos*, *Amphicyon*, *Megistotherium*, *Hyainailouros* Stehlin, 1907 (Table 2). Even if *Megistotherium* is subsumed into *Hyainailouros* (Morlo et al. 2007; Morales & Pickford 2017), *Afrocyon* from Gebel Zelten represents a fourth large taxon, and the number of Early Miocene large carnivore species and genera recognized has probably not yet reached its zenith. For example, more work remains to be done on the possible phoberocyonine ursid from Rusinga (Werdelin & Peigné 2010), and the giant *Cynelos* from Buluk (Anemone *et al.* 2005).

Morphological differences evident among the early Miocene large carnivores suggest that *Cynelos*, with its more trenchant form, was the most carnivorous Early Miocene amphicyonid of Africa, while *Amphicyon*, *Hyainailouros*, and *Megistotherium,* which show evidence of abrasive horizontal wear, had more bone-crushing capabilities (Morales *et al.* 2003; Morlo *et al.* 2007). Beyond these observations, the ecomorphological variables that would have permitted the co-existence of these giants are not well understood. The structure of the Early Miocene carnivore guild of Africa has no known analog, but it is perhaps instructive that this is also true of some other Early Miocene lineages. For example, the Early Miocene fossil record of proboscideans and hominoids also documents a richness and abundance that contrasts with the taxonomically impoverished character of these lineages today.

Members of the order Carnivora appear to be among the earliest immigrant groups to arrive in Africa after the collision of the Afro-Arabian and Eurasian tectonic plates *c.* 23 Ma (Billups *et al.* 2004; Ogg 2012; Hunt & Stepleton 2015). Before the Miocene, Africa was an island continent with a largely endemic fauna, and in this fauna the apex predators were hyainailourine hyaenodontids rather than carnivorans. Evidence in support of the early arrival of Carnivora into Africa includes the recovery of the stenoplesictid, *Mioprionodon hodopeus,* from the earliest Miocene of Kenya (*c.* 22.5 Ma) (Rasmussen & Gutiérrez 2009). However, the docking of Afro-Arabia with Eurasia must have been preceded by epicontinental sea conditions, which might have permitted some lineages to arrive in Africa before completion of a land bridge, a view that may be supported if further work continues to document the presence of a probable amphicyonid among the late Oligocene fauna of Angola (Hooijer 1963).

Acknowledgements

We thank Louis de Bonis for inviting us to contribute to this memorial volume in honor of Stéphane Peigné. Three of us published with Stéphane, and always benefited from his deep knowledge and passion for carnivore evolution, as well as from his gentle personality. We thank the Government of Egypt, and the Egyptian Geological Survey and Mining Authority for permission to work at Moghra, and Jeff Nichols, Wake Forest University, for help with figures. Field and museum research were supported by awards from the National Science Foundation (E.R.M., A.N, el-B.), The Leakey Foundation, The Boise Fund of Oxford University, Sigma Xi, and the Archie Fund of Wake Forest University. We also thank Jorge Morales for providing the collection number of the partial mandible of *Cynelos anubisi* n. sp. from Gebel Zelten. Lars Werdelin, Robert M. Hunt and an anonymous reviewer largely increased the quality of the manuscript.

REFERENCES

AbdelGawad M. K. 2011. — *Geological and Paleoecological aspects of the Moghra Fossil Mammals, North Western Desert, Egypt.* Master Thesis, Geology Department, Faculty of Science, Cairo University, 211 p.

AbdelGawad M. K., Miller E. R., Hamdan M. A., Ali S. M., El-Sharkawy M. A. & El-Barkooky A. N. 2010. — *Stratigraphic Distribution of Fossil Mammals in the Early Miocene Moghra Formation, North Western Desert, Egypt.* The 10th International Conference on Geology of the Arab World (GAW10), Cairo University, Egypt.

AbdelGawad M. K., Miller E. R., Hamdan M. A., El-Barkooky A. N. & El-Sharkawy M. A. 2012. — Vertebrate and geological signatures on the construction of Moghra formation, North Western Desert, Egypt. *Journal of Vertebrate Paleontology* 32 (Supplement 2, Program and Abstracts): 54.

Adrian B., Werdelin L. & Grossman A. 2018. — New Miocene Carnivora (Mammalia) from Moruorot and Kalodirr, Kenya. *Palaeontologia Electronica* 21.1.10a 1-19. https://doi.org/10.26879/778.

Anemone R., Grossman A., Miller E. R. & Watkins R. 2005. — Biochronology and paleoecology of the Buluk fauna, Early Miocene of northern Kenya. *Journal of Vertebrate Paleontology* 25 (3, Supplement): 32A. https://doi.org/10.1080/02724634.2005.10009942

Arambourg C. 1961. — Note préliminaire sur quelques Vertébrés nouveaux du Burdigalien de Libye. *Compte rendu de la Société Géologique de France* 4: 107, 108.

Bastl K., Nagel D., Morlo M. & Göhlich U. B. 2018. — The Carnivora (Mammalia) from the middle Miocene locality of Gračanica (Bugojno Basin, Gornji Vakuf, Bosnia and Herzegovina). *Palaeobiodiversity and Palaeoenvironments*: 1-13. https://doi.org/10.1007/s12549-018-0353-0

Behrensmeyer A. K., Deino A. L., Hill A., Kingston J. D. & Saunders J.J. 2002. — Geology and geochronology of the middle Miocene Kipsaramon site complex, Muruyur Beds, Tugen Hills, Kenya. *Journal of Human Evolution* 42: 1-38. https://doi.org/10.1006/jhev.2001.0519

Billups K., Pälike H., Channell J. E. T., Zachos J. C. & Shackleton N. J. 2004. — Astronomic calibration of the late Oligocene through early Miocene geomagnetic polarity time scale. *Earth and Planetary Science Letters* 224: 33-44. https://doi.org/10.1016/j.epsl.2004.05.004

Bonis L. de 2013. — Ursidae (Mammalia, Carnivora) from the Late Oligocene of the "Phosphorites du Quercy" (France) and a reappraisal of the genus *Cephalogale* Geoffroy, 1862. *Geodiversitas* 35 (4): 787-814. https://doi.org/10.5252/g2013n4a4.

Bowdich T. E. 1821. — *An Analysis of the Natural Classifications of Mammalia, for the use of Students and Travelers*. J. Smith, Paris, 115 p. https://archive.org/details/bub_gb_wVgQAQAAMAAJ

Cuvier G. 1824. — *Recherches sur les Ossemens fossils où l'on rétablit les caractères de plusieurs animaux dont les revolutions du globe ont détruit les espèces.* 2nd edition. G. Dufour et E. d'Ocagne, Paris. https://doi.org/10.5962/bhl.title.122964

Drake R. E., Van Couvering J. A., Pickford M. H., Curtis G. H. & Harris J. A. 1988. — New chronology for the Early Miocene mammalian faunas of Kisingiri, Western Kenya. *Journal of the Geological Society* 145: 479-491. https://doi.org/10.1144/gsjgs.145.3.0479

Fejfar O. & Heizmann E. 2016. — An illustrated summary of the lower Miocene carnivores (Mammalia, Carnivora) of Tuchořice, Czech Republic. *Historical Biology* 28 (1-2): 316-329. https://doi.org/10.1080/08912963.2015.1029923

Figueirido B., Pérez-Claros J. A., Hunt R. M. Jr & Palmqvist P. 2011. — Body mass estimation in amphicyonid carnivoran mammals: A multiple regression approach from the skull and skeleton. *Acta Palaeontologica Polonica* 56 (2): 225-246. https://doi.org/10.4202/app.2010.0005

Gagnaison C., Cossard B. & Dechamps M. 2017. — À propos de quelques dents et os de Mammifères Carnivores du Miocène de l'Anjou-Touraine. *Symbioses, nouvelle série* 35-36: 47-60.

Gebo D. L., MacLatchy L., Kityo R., Deino A. L., Kingston J. D. & Pilbeam D. 1997. — A Hominoid Genus from the Early Miocene of Uganda. *Science* 276: 401-404. https://doi.org/10.1126/science.276.5311.401

Ginsburg L. 1977. — *Cynelos lemanensis* (Pomel), carnivore ursidé de l'Aquitanien d'Europe. *Annales de Paléontologie, Vertébrés* 63 (1): 57-104.

Ginsburg L. 1980. — *Hyainailouros sulzeri*, mammifère créodonte du Miocène d'Europe. *Annales de Paléontologie, Vertébrés*, 66 (1): 19-73.

Ginsburg L. & Antunes M. T. 1995. — Les carnivores du miocène de Lisbonne (Portugal). *Annales de Paléontologie* 81 (3): 125-165.

Ginsburg L. & Bulot C. 1982. — Les carnivores du miocène de Bézian près de la Romieu (Gers, France). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschapen, Series B* 85 (1): 53-76.

Ginsburg L. & Telles-Antunes M. 1968. — *Amphicyon giganteus*, carnassier géant du Miocène. *Annales de Paléontologie* 54 (1): 1-32.

Ginsburg L. & Welcomme J.-L. 2002. — Nouveaux restes de Créodontes et de Carnivores des Bugti (Pakistan). *Symbioses* (n.s.) 7: 65-68.

Haeckel E. 1866. — *Generelle Morphologie der Organismen*. Volume 2. Georg Reimer, Berlin, 462 p. https://doi.org/10.5962/bhl.title.3953

Hassan S. M., Steel R. J., El-Barkooky A. N., Hamdan M. A., Olariu C. & Helper M. A. 2012. — Stacked, Lower Miocene tide-dominated estuary deposits in a transgressive succession, Western Desert, Egypt. *Sedimentary Geology* 282: 241-255. https://doi.org/10.1016/j.sedgeo.2012.09.013

Hassan S. M. 2013 — *Sequence Stratigraphy of the Lower Miocene Moghra Formation in the Qattara Depression, North Western Desert, Egypt*. SpringerBriefs in Earth Sciences, New York, 160 p. https://doi.org/10.1007/978-3-319-00330-6

Hendey Q. B. 1978. — Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Annals of the South African Museum* 76: 1-41. http://www.biodiversitylibrary.org/page/40697468

Hill A., Drake R., Tauxe L., Monaghan M., Barry J., Behrensmeyer K., Curtis G., Jacobs B., Jacobs L., Johnson N. & Pilbeam D. 1985. — Neogene palaeontology and geochronology of the Baringo Basin, Kenya. *Journal of Human Evolution* 14: 749-773. https://doi.org/10.1016/S0047-2484(85)80058-0

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

Hunt R. M. Jr 1998. — Amphicyonidae *in* Janis C. M., Scott K. M. & Jacobs L. L. (eds), *Evolution of Tertiary Mammals of North America Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals.* Volume 1. Cambridge University Press, Cambridge: 196-227.

Hunt R. M. Jr & Stepleton E. 2015. — A Skull of the Immigrant Eurasian Beardog *Cynelos* (Carnivora, Amphicyonidae) from the Early Miocene of Southern California. *Journal of Vertebrate Paleontology* 35 (1) e891229: 1-19. https://doi.org/10.1080/02724634.2014.891229

Jiangzuo Q., Chunxiao L., Zhang X., Wang S., Ye L. & Li Y. 2018. — Diversity of Amphicyonidae (Carnivora, Mammalia) in the Middle Miocene Halamagai formation in Ulungur River area, Xinjiang, Northwestern China. *Historical Biology*, https://doi.org/10.1080/08912963.2018.1477142

Jiangzuo Q., Chunxiao L., Zhang X., Wang S. & Sun D. 2019. — A*mphicyon zhanxiangi*, sp. nov., a new amphicyonid (Mammalia, Carnivora) from northern China. *Journal of Vertebrate Paleontology* e1539857. https://doi.org/10.1080/02724634.2018.1539857

Jourdan C. 1862. — Des terrains sidérolitiques. *Revue des Sociétés savantes. Sciences mathématiques, physiques et naturelles, Paris* 1: 130-133. https://gallica.bnf.fr/ark:/12148/bpt6k202286k/f135.item

Kuss S. E. 1965. — Revision der europäischen Amphicyoninae (Canidae, Carnivora, Mamm.) ausschliesslich der voroberstampischen Formen. *Sitzungsberichte der Heidelberger Akademie der Wissenschaften* 1: 5-168.

Leakey M., Grossmann A., Gutiérrez M. & Fleagle J. G. 2011. — Faunal Change in the Turkana Basin during the Late Oligocene and Miocene. *Evolutionary Anthropology* 20: 238-253. https://doi.org/10.1002/evan.20338

Lukens W. E., Lehmann T., Peppe D. J., Fox D. L., Driese S. G. & McNulty K. P. 2017. — The Early Miocene critical zone at Karungu, western Kenya: An equatorial, open habitat with few primate remains. *Frontiers in Earth Science* 5: 87. https://doi.org/10.3389/feart.2017.00087

Michelin J. L. H. 1836. — Notes sur les ossemens et coquilles fossiles trouvés dans un terrain d'eau douce à Simorre et Sansan. *Bulletin de la Société géologique de France* 7: 217-220.

Miller E. R. 1999. — Faunal correlation of Wadi Moghara, Egypt: implications for the age of *Prohylobates tandyi*. *Journal of Human Evolution* 36 (5): 519-533. https://doi.org/10.1006/jhev.1998.0286

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

Morales J. & Pickford M. 2008. — Creodonts and carnivores from the Middle Miocene Muruyur Formation, Kipsaraman and Cheparawa, Baringo District, Kenya. *Comptes Rendus Palevol* 7: 487-497. https://doi.org/10.1016/j.crpv.2008.09.011

Morales J. & Pickford M. 2017. — New hyaenodonts (Ferae, Mammalia) from the Early Miocene of Napak (Uganda), Koru (Kenya) and Grillental (Namibia). *Fossil Imprint* 73 (3-4): 332-359. https://doi.org/10.2478/if-2017-0019

Morales J., Pickford M., Soria D. & Fraile S. 1998. — New carnivores from the basal Middle Miocene of Arrisdrift, Namibia. *Eclogae Geologicae Helvetiae* 91 (1): 27-40.

Morales J., Pickford M., Fraile S., Salesa M. J. & Soria D. 2003. — Creodonta and Carnivora from Arrisdrift, early Miocene of Southern Namibia. *Memoirs of the Geological Survey of Namibia* 19: 177-194.

Morales J., Pickford M. & Soria D. 2005. — Carnivores of 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. & Salesa M. J. 2008. — Creodonta and Carnivora from the early Miocene of the Northern Spergebiet, Namibia. *Memoir of the Geological Survey of Namibia* 20: 291-310.

Morales J., Pickford M. & Soria D. 2007. — New carnivores (Creodonta and Carnivora) from the Early Miocene of Napak, Uganda. *Paleontological Research* 11: 71-84. https://doi.org/10.2517/1342-8144(2007)11[71:NCMCCA]2.0.CO;2

Morales J., Brewer P. & Pickford M. 2010. — Carnivores (Creodonta and Carnivora) from the basal middle Miocene of Gebel Zelten, Libya, with a note on a large amphicyonid from the middle Miocene of Ngorora, Kenya. *Bulletin of the Tethys Geological Society* 5: 43-54.

Morales J., Pickford M. & Valenciano A. 2016. — Systematics of African Amphicyonidae, with descriptions of new material from Napak (Uganda) and Grillental (Namibia). *Journal of Iberian Geology* 42 (2): 131-150. http://hdl.handle.net/10261/137042

Morlo M., Miller E. R. & El-Barkooky A. N. 2007. — Creodonta and Carnivora from Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology* 27 (1): 145-159. https://doi.org/10.1671/0272-4634(2007)27[145:CACFWM]2.0.CO;2

Nagel D., Stefen C. & Morlo M. 2009. — The carnivoran community from the Miocene of Sandelzhausen (Germany). *Paläontologische Zeitschrift* 83: 151-174. https://doi.org/10.1007/s12542-009-0008-6

Ogg J. G. 2012. — Geomagnetic polarity time scale, *in* Gradstein F. M., Ogg J. G., Schmitz M. D. & Ogg G. M. (eds), *The Geologic Time Scale 2012*. Elsevier, Amsterdam: 85-114.

Peigné S. 2012. — Les Carnivora de Sansan, *in* Peigné S. & Sen S. (eds), *Mammifères de Sansan*. Muséum national d'Histoire naturelle, Paris: 559-660 (Mémoires du Muséum national d'Histoire naturelle ; 203).

Peigné S. & Heizmann E. P. J. 2003. — The Amphicyonidae (Mammalia: Carnivora) from Ulm-Westtangente (MN 2, Early Miocene), Baden Württemberg, Germany – systematics and ecomorphology. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* 343: 1-133.

Peigné S., Chaimanee Y., Yamee C., Tian P. & Jaeger J.-J. 2006a. — A new amphicyonid (Mammalia, Carnivora, Amphicyonidae) from the late middle Miocene of northern Thailand and a review of the amphicyonine record in Asia. *Journal of Asian Earth Sciences* 26 (5): 519-532. https://doi.org/10.1016/j.jseaes.2004.11.003

Peigné S., Salesa M. J., Antón M. & Morales J. 2006b. — New data on carnivores from the Middle Miocene (Upper Aragonian, MN 6) of Arroyo del Val area (Villafeliche, Zaragoza Province, Spain). *Estudios Geológicos* 62 (1): 359-374.

Peigné S., Salesa M. J., Antón M. & Morales J. 2008. — A new Amphicyonine (Carnivora: Amphicyonidae) from the Upper Miocene of Batallones-1, Madrid, Spain. *Paleontology* 51 (4): 943-965. https://doi.org/10.1111/j.1475-4983.2008.00788.x

Peppe D. J., Deino A. L., McNulty K. P., Lehmann T., Harcourt-Smith W. E. H., Dunsworth H. M. & Fox D. L. 2011. — New age constraints on the early Miocene faunas from Rusinga and Mfangano Islands (Lake Victoria, Kenya). *American Journal of Physical Anthropology* 144 (Suppl): 237. https://doi.org/10.1002/ajpa.21502

Peppe D. J., McNulty K. P., Deino A. L., Michel L. A., McCollum M. S., Driese S. G., Dunsworth H. M., Harcourt-Smith W. E. H., Jenkins K. E. & Lehmann T. 2016. — Early Miocene paleoenvironments of the Hiwegi Formation on Rusinga Island (equatorial Africa and Victoria, Africa, Lake Victoria, Kenya) and their implications for hominoid evolution. *Geological Society of America* 48(7). https://doi.org/10.1130/abs/2016AM-280981

Peppe D. J., Deino A. L., McNulty K. P., McCollum M. S., Mitchell A. L., Driese S. G., Dunsworth H. M., Fox D. L., Harcourt-Smith W. E. H., Jenkins K. Lehmann T. & Michel L. A. 2017. — Revised geochronology of the Early Miocene faunas from Rusinga Island and Mfangano Island (Lake Victoria, Kenya): Implications for Miocene hominoid evolution and faunal succession. *American Journal of Physical Anthropology Programs and Abstracts* 2017: 313.

Pickford M. 1986. — Cainozoic paleontological sites of Western Kenya. *Münchner Geowissenschaftliche Abhandlungen* A8: 1-151.

Pickford M. 1991. — Revision of Neogene Anthracotheriidae of Africa *in* Salem M. J. (ed.), *The Geology of Libya.* Volume 4. Elsevier, Amsterdam: 1491-1525.

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. https://doi.org/10.1016/j.crpv.2003.10.001

Pomel A. 1846. — Mémoire pour servir à la géologie paléontologique des terrains tertiaires du département de l'Allier. *Bulletin de la Société géologique de France,* série 2, 3: 353-373. https://biodiversitylibrary.org/page/54306487

Rasmussen D. T. & Gutierrez M. 2009. — A mammalian fauna from the Late Oligocene of Northwestern Kenya. *Palaeontographica Abteilung A* 288:1-52. https://doi.org/10.1127/pala/288/2009/1

Sanders W. J., Kappelman J. & Rasmussen D. T. 2004. — New large bodied mammals from the late Oligocene site of Chilga, Ethiopia. *Acta Palaeontologica Polonica* 49: 365-392.

Sanders W. J. & Miller E. R. 2002. — New Proboscideans from the Early Miocene of Wadi Moghra, Egypt. *Journal of Vertebrate Paleontology* 22 (2): 388-404. https://doi.org/10.1671/0272-4634(2002)022[0388:NPFTEM]2.0.CO;2

Savage R. J. G. 1965. — Fossil mammals of Africa: 19. The Miocene Carnivora of East Africa. *Bulletin of the British Museum of Natural History (Geology)* 10 (8): 239-316. http://www.biodiversitylibrary.org/page/36359760

Savage R. J. G. 1973. — *Megistotherium*, gigantic hyaenodont from Miocene of Gebel Zelten, Libya. *Bulletin of the British Museum of Natural History (Geology)* 22: 483-511. http://www.biodiversitylibrary.org/page/36949982

Savage R. J. G. & Hamilton W. R. 1973. — Introduction to the Miocene mammal faunas of Gebel Zelten, Libya. *Bulletin of the British Museum of Natural History (Geology)* 22 (8): 515-527. http://www.biodiversitylibrary.org/page/36950026

Schinz H. R. 1825. — *Das Thierreich eingetheilt nach dem Bau der Thiere als Grundlage ihrer Naturgeschiechte und der vergleichenden Anatomie von dem Herrn Ritter von Cuvier*. Volume 4. Stuttgart and Tübingen, 792 p. https://doi.org/10.5962/bhl.title.120160

Schlosser M. 1899. — Über die Bären und bärenähnlichen Formen des europäischen Tertiärs. *Palaeontographica, Abteilung A* 46: 95-148.

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

Smith J. B. & Dodson P. 2003. — A proposal for a standard terminology of anatomical notation and orientation in fossil vertebrate dentitions. *Journal of Vertebrate Paleontology* 23 (1): 1-12. https://doi.org/10.1671/0272-4634(2003)23[1:APFAST]2.0.CO;2

Sorkin B. 2006. — Ecomorphology of the giant bear-dogs *Amphicyon* and *Ischyrocyon*. *Historical Biology* 18 (4): 375-388. https://doi.org/10.1080/08912960600618073

Tomiya S. & Tseng Z. J. 2016. — Whence the beardogs? Reappraisal of the Middle to Late Eocene '*Miacis*' fromTexas, USA, and the origin of Amphicyonidae (Mammalia, Carnivora). *Royal Society Open Science* 3: 160518. https://doi.org/10.1098/rsos.160518

Trouessart E. L. 1885. — *Catalogue des mammifères vivants et fossiles (carnivores)*. Germain et G. Grassin, Angers, 108 p. https://doi.org/10.5962/bhl.title.63808

Van Valen M. 1994. — Serial homology: the crests and cusps of mammalian teeth. *Acta Palaeontologica Polonica* 38 (3/4): 145-158.

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

Wang X., Hunt R. M. Jr, Tedford R. H. & Lander E. B. 2009. — First record of immigrant Phoberogale (Mammalia, Ursidae, Carnivora) from Southern California. *Geodiversitas* 31 (4): 753-773. https://doi.org/10.5252/g2009n4a753

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

Werdelin L. & Peigné S. 2010. — Carnivora *in* Werdelin L. & Sanders W. J. (eds), *Cenozoic Mammals of Africa*. University of California Press: 603-657.

Werdelin L. & Simpson S. W. 2009. — The last amphicyonid (Mammalia, Carnivora) in Africa. *Geodiversitas* 31 (4): 775-787. https://doi.org/10.5252/g2009n4a775

Wuthrich C., MacLatchy, L. M. & Nengo I. O. 2019. — Wrist morphology reveals substantial locomotor diversity among early catarrhines: an analysis of capitates from the early Miocene of Tinderet (Kenya). *Scientific Reports* 9 (3728): 1-10. https://doi.org/10.1038/s41598-019-39800-3

Whybrow P. J. 1984. — Geological and faunal evidence from Arabia for mammal "migrations" between Asia and Africa during the Miocene. *Courier Forschungsinstitut Senckenberg* 69: 189-198.

Submitted on 12 December 2018;
accepted on 3 June 2019;
published on 7 November 2019.