The taxonomic status of "*Ysengrinia*" *ginsburgi* Morales *et al*. 1998 (Amphicyonidae, Carnivora) from the basal middle Miocene of Arrisdrift, Namibia

Jorge Morales[1] & Martin Pickford[2]

1. Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC - C/José Gutiérrez Abascal 2, 28006, Madrid, Spain (jorge.morales@mncn.csic.es)
2. Sorbonne Université - CR2P, MNHN, CNRS, UPMC - Paris VI, 8, rue Buffon, 75005, Paris, France (martin.pickford@mnhn.fr)

Abstract :- The aim of this article is to revise the taxonomic status of *Ysengrinia ginsburgi* Morales *et al*. 1998. This species of amphicyonid carnivore was defined on the basis of specimens from the early Miocene locality of Arrisdrift, Namibia. It was subsequently transferred to the genus *Afrocyon* Arambourg, 1961, by Morales *et al*. (2006) and more recently was included by Morlo *et al*. (2019) in the genus *Cynelos* Jourdan, 1862, as *C. ginsburgi*, along with a new species *Cynelos anubisi* from the locality of Moghara, Egypt. Morphological and biometric analyses of the dentition of the two African species indicate that they do not belong to the genus *Cynelos*, of which the type species, *C. lemanensis* shows a hypocarnivorous dental adaptation, the opposite of the situation in the species from Namibia and Egypt, both of which are hypercarnivorous. The latter two species are clearly distinct from *Afrocyon burolleti* Arambourg, 1961, from Gebel Zelten, Libya, and their dentitions show differences that indicate that we are in the presence of distinct genera; *Namibiocyon* nov. gen. g*insburgi* (Morales *et al*.) 1998, for the species from Arrisdrift, Namibia, and *Mogharacyon* nov. gen. *anubisi* (Morlo *et al*. 2019) for the species from Moghara.

KeyWords :- Ferae, Carnivora, early Miocene, Namibia, Egypt, taxonomy

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Introduction

The Amphicyonidae first appear in the African fossil record at the beginning of the early Miocene and persisted until the end of the Miocene, a few million years after their extinction in Eurasia and North America. In contrast to their diversity and abundance in the European and North American fossil records, the group is generally poorly represented in African localities. This could be related to the limited quantity of African localities, but it might also be related to the fact that hyaenodonts were highly diverse in Africa during the early and middle Miocene (Morales *et al*. 2017).

The systematics of African Amphicyonidae have been actively debated ever since the description of the first autochthonous taxon, *Afrocyon burolleti* Arambourg, 1961, a species based on an incomplete mandible from the basal middle Miocene locality of Gebel Zelten (Libya), that suffered from sand-blasting after eroding from the deposits in which it was fossilised. A few years later the description of *Hecubides euryodon* Savage, 1965, extended the representation of the group downwards in time to the base of the early Miocene at Napak I and Napak IV (Uganda) and localities in Kenya. Ginsburg (1980) in his revision of *Hyainailouros*, cited for the first time, in a list of carnivores from East Africa, a new combination for the species of *Hecubides* as *Cynelos euryodon* and *Cynelos macrodon*, but without any explanation. He also cited *Cynelos bugtiensis* (Forster Cooper, 1923) in the list of carnivorans from Bugti but this is a *lapsus calami*, as he probably meant *Cephalogale bugtiensis* Forster Cooper 1923. Schmidt-Kittler (1987) accepted this change of genus indicating that the species *Amphicyon*

lemanensis Pomel 1846, should be included in the genus *Cynelos* Jourdan, 1862. These arguments led to the suggestion that the African species should be classified as *Cynelos euryodon* (Savage, 1965).

A third genus *Myacyon dojambir* Sudre & Hartenberger, 1992, from the late Miocene of Algeria, in which the dimensions of the m/1 are close to the largest specimens of *Megamphicyon giganteus* from Europe, is characterised by the presence of a relatively small m/2 compared to the m/1. This suggests that it evolved from a different evolutionary lineage from that of the giant amphicyonids of Europe, and that it was possibly derived directly from the middle Miocene African forms previously classified in, or related to, the genus *Agnotherium* Kaup, 1832 (Morales *et al*. 2016 and references cited therein). Finally, *Bonisicyon illacabo* Werdelin & Simpson, 2009, represents the most recent record of the Amphicyonidae in Africa, a genus characterised by its small dimensions and peculiar morphology making it difficult to relate to other species of the family.

Revisions of African Amphicyonidae were made by Werdelin & Peigné (2010) and Morales *et al*. (2016). More recently Adrian *et al*. (2018) and Werdelin (2019) described new materials from the Kenyan localities of Kalodirr and Fort Ternan. Morlo *et al*. (2019) described new amphicyonid fossils from Moghara, Egypt, identifying them as *Cynelos anubisi* nov. sp. and *Amphicyon giganteus*. These authors disagreed with the attribution of the medium-sized species from Arrisdrift by Morales *et al*. (2016) to *Afrocyon* suggesting that it belongs instead to *Cynelos* Jourdan, 1862, as the new combination *Cynelos ginsburgi* (Morales *et al*. 1998). This revision profoundly altered the taxonomic grouping proposed by Morales *et al*. (2016). For Morlo *et al*. (2019) *Afrocyon burolleti* should be restricted to material from the type locality, Gebel Zelten, the larger form from Arrisdrift should be maintained in "*Amphicyon*" *giganteus*, which includes fossils from Gebel Zelten and Moghara. The remainder of the species from the early and middle Miocene of Africa – spanning the period ca 21 Ma to ca 15 Ma – are classified in the genus *Cynelos* Jourdan, 1862, such that it includes *Cynelos euryodon* (Savage 1965); *Cynelos minor* (Morales & Pickford, 2008), *Cynelos macrodon* (Savage 1965); *Cynelos anubisi* Morlo *et al.* 2019 and *Cynelos jitu* Morlo *et al*. 2021, a giant species from Buluk (Kenya) (see Morlo *et al*. 2019, table 2).

The aim of the present work is to discuss the taxonomic status of the Arrisdrift species originally identified as *Ysengrinia ginsburgi* Morales *et al*. 1998, in the light of new studies on the Amphicyonidae published subsequent to the work of Morales *et al*. (2016).

Arrisdrift Amphicyonidae

The locality of Arrisdrift (Sperrgebiet) Namibia, has yielded a rich and diverse assemblage of vertebrates correlated to the end of the early Miocene and beginning of the middle Miocene (ca 17-17.5 Ma) being by far the richest known from the southern third of the African continent (Pickford *et al*. 1996; Pickford & Senut, 1999, 2003).

The Amphicyonidae from Arrisdrift were first studied by Hendey (1978) who identified two forms on the basis of two relatively complete mandibles. One is the same size as *Amphicyon* cf. *steinheimensis* and the other, which is much larger, was attributed to Amphicyonidae gen. et sp. indet. The material was revised by Morales *et al*. (1998, 2003) to which were added new fossils excavated by the Namibia Palaeontology Expedition from 1993-2000. The medium-sized form was identified as *Ysengrinia ginsburgi* Morales *et al*. 1998, whereas the larger form was attributed to *Amphicyon giganteus* (Schinz, 1825). These identifications were maintained until the revision of Morales *et al*. (2016), who transferred the medium-sized form to the genus *Afrocyon*, as the combination *Afrocyon ginsburgi* (Morales *et al*. 1998) and the larger form to the genus *Megamphicyon* as *Megamphicyon giganteus* (Schinz, 1825). Morlo *et al*. (2019) transferred *Afrocyon ginsburgi* to the genus *Cynelos*, proposing the new combination *Cynelos ginsburgi* (Morales *et al*. 1998).

Institutional Abbreviations

CUWM - Cairo University, Moghara collection, Cairo, Egypt
DPC - Duke University Primate Center, Division of Fossil Primates, Durham, North Carolina, USA
FSL - Faculté des Sciences, Université Claude Bernard 1, Lyon, France
GSN - Geological Survey of Namibia, Windhoek, Namibia
MNHN - Museum national d'Historie naturelle, Paris, France;
NHMUK - Natural History Museum, London, United Kingdom
UM - Uganda Museum, Kampala, Uganda

Other Abbreviations

L - mesiodistal diameter
W - buccolingual width
AD - Arrisdrift locality
NAP - Napak localities
SG - Saint Gérand le Puy

Systematic Palaeontology

Order Carnivora Bowdich, 1821

Family Amphicyonidae Trouessart, 1885

Subfamily Amphicyoninae Trouessart, 1885

Tribe Amphicyonini Trouessart, 1885

Remarks :- This tribe includes the most typical Amphicyoninae; its molar dentition tends to present an increased surface, the carnassials are robust and the premolar dentition progressively decreases in size and complexity (Morales *et al*. 2021). In Europe the included genera are:- *Amphicyon* Lartet, 1837; *Cynelos* Jourdan, 1862; *Paludocyon* Morales *et al*. 2021; *Heizmannocyon* Ginsburg, 1999; *Megamphicyon* Kuss, 1965 and *Euroamphicyon* Viranta, 1996. In Africa included genera are:- *Afrocyon* Arambourg, 1961; *Hecubides* Savage, 1965; *Myacyon* Sudre & Hartenberger, 1992; *Bonisicyon* Werdelin & Simpson, 2009; *Namibiocyon* nov. gen. and *Mogharacyon* nov. gen. The European genera *Cynelos* Jourdan, 1862, *Amphicyon* Lartet, 1837 (including *Megamphicyon* Kuss, 1965) and the Thaumastocyoninae *Agnotherium* Kaup, 1832, have been repeatedly recorded from some African sites (Werdelin & Peigné, 2010; Morlo *et al*. 2019).

Genus *Namibiocyon* nov.

Type species :- *Namibiocyon ginsburgi* (Morales *et al*. 1998)

Type locality :- Arrisdrift, Sperrgebiet, Namibia.

Age :- Basal middle Miocene.

Diagnosis :- Medium-sized Amphicyonini (Length m/1 27-29 mm); elongated mandible with complete premolar series; premolars reduced, biradiculate p/4-p/2, diastemata between p/3-p/2, p/2-p/1 and p/1-c/1; p/4 small with mesial cuspid reduced to absent, distal cuspid well-developed, widened talonid surrounded by a strong cingulum; m/1 tall and compressed bucco-lingually with reduced metaconid, short talonid dominated by a tall and broad hypoconid, small entoconid, reduced to a

low crenulated crest; m/2 relatively short with respect to m/1, with tall trigonid in which the paraconid is reduced, the narrow talonid dominated by the hypoconid and a much reduced entoconid; m/3 simple, with the protoconid individualised, and paraconid and metaconid united in a mesio-lingual crest , narrow talonid; P3/ much reduced; P4/ with paracone compressed transversely with a strong mesial crista, parastylar region enlarged. The metastyle is short but is mesio-distally aligned with the paracone. The protocone is much reduced and backs onto the mesio-lingual base of the paracone. The flexus is clearly developed in the mesial wall between the protocone and the base of the parastyle. A basal cingulum completely surrounds the tooth and is especially strong at the lingual base of the metastyle; M1/ subtriangular, paracone much larger and taller than the metacone; parastyle and metastyle very small, moderate buccal cingulum; Paraconule and metaconule strong, the protocone duniform, well-developed and displaced mesially. The lingual cingulum is very strong, but is limited to the disto-lingual border. The alveoli of M2/ indicate that the tooth was mesio-distally short, but was as well-developed bucco-lingually as the M1/; d/3 with small mesial cuspids, main cusp tall and pointed, broad talonid with tall cingulum; d/4 with tall protoconid, compressed bucco-lingually, small metaconid, short talonid with tall hypoconid and strong cristid obliqua, lateral crest of the entoconid united to the base of the metaconid, and separated distally from the hypoconid.

Species *Namibiocyon ginsburgi* (Morales *et al.* 1998).

Synonymy :-

1978 *Amphicyon* cf. *steinheimensis* Hendey, p. 10.
1998 *Ysengrinia ginsburgi* Morales *et al*. p. 30.
2002 *Ysengrinia ginsburgi* Hunt, p. 14.
2003 *Ysengrinia ginsburgi* Morales *et al*. p. 178.
2010 *Ysengrinia ginsburgi* Werdelin & Peigné, p. 606.
2016 *Afrocyon ginsburgi* Morales *et al*. p. 141.
2019 *Cynelos ginsburgi* Morlo *et al*. p. 732

Holotype :- GSN AD 133, left mandible (Hendey, 1978, Fig. 3; Morales *et al*. 1998, Fig.3; Morales *et al*. 2003, Pl. 3, Fig. 1).

Type locality :- Arrisdrift, Sperrgebiet, Namibia

Age :- Terminal early Miocene

Diagnosis :- As for the genus.

Discussion

The presence of an unreduced M2/ in the maxilla GSN AD 606'94 from Arrisdrift originally attributed to *Ysengrinia ginsburgi* by Morales *et al*. (1998, 2003) highlights the difficulty of classifying this species in the genus *Ysengrinia* Ginsburg, 1965 (Morales *et al*. 2016); this genus is currently considered to be one of the most basal taxa of the subfamily Thaumasto-cyoninae Hürzeler, 1940 (Morales *et al*. 2019, 2021). The alternative proposed by Morales *et al*. (2016) to classify it as *Afrocyon ginsburgi* was recently contested by Morlo *et al*. (2019) who proposed the new taxonomic combination *Cynelos ginsburgi* (Morales *et al*. 1998).

Namibiocyon ginsburgi shows a grade of evolution comparable to *Afrocyon burolleti* Arambourg, 1961 (included in this species is the new material from Gebel Zelten described by Morales *et al*. 2016). At the time of the study, the authors focussed more on the similarities shared by the two taxa, rather than the differences between them, opting to include them in the same genus. However, *Namibiocyon ginsburgi* shows important differences from *A. burolleti*, such as; i) more reduced p/4, with a vertical main cusp and a broader talonid, ii) more sectorial m/1 due to reduction of the metaconid, and the shorter talonid almost completely occupied by a tall hypoconid aligned with the protoconid and paraconid,

iii) small m/2 with very narrow talonid that, as in the m/1, is comprised of a hypertrophied hypoconid, iv) less reduced m/3 (Figs 1-5).

These differences, even though limited to the lower dentition, are sufficiently great to indicate separation of the two species at the genus level. Because of this we erect the new genus *Namibiocyon*, characterised by a more hypercarnivorous dentition than occurs in the species of *Afrocyon*.

The suggestion by Morlo *et al*. (2019) to include the Arrisdrift species in *Cynelos* Jourdan, 1862, is difficult to retain, independent of the taxonomic controversy concerning the validity of this genus for the African species (Schmidt-Kittler 1987; Werdelin & Peigné, 2010; Adrian *et al*. 2018) in place of *Hecubides* Savage, 1965 (Morales *et al*. 2007, 2008, 2016). In particular, *Cynelos lemanensis* (Pomel, 1846) the type species of the genus, combines derived features such as the large dimensions and subquadrangular morphology of the upper molars (M1/-M2/) (Fig. 2), with primitive characters such as the low buccal cusplets in the upper molars, the morphology of the P4/ which retains quite a strong protocone and is above all short with respect to the molars. In the lower dentition, comparable characters occur, despite the fact that the mandible retains two-rooted premolars that are barely reduced, the shredding dentition (talonid of m/1, m/2 and m/3) is well developed in agreement with the great development of the occlusal surface of the upper molars. These features distance *Cynelos lemanensis* from the most primitive forms of the family that are clearly hypercarnivorous, and for the same reasons, from the groups more derived towards this specialisation such as Haplocyoninae de Bonis (1966) and Thaumastocyoninae (Morales *et al*. 2019). The morphology and development of the molars of *Cynelos lemanensis* show convergences towards Pseudarctini Morales *et al*. 2021 (Figs 3-5), but they differ from them by the lack of reduction of the size of the carnassial teeth. *Namibiocyon ginsburgi* clearly represents a grade of specialisation opposed to that of *Cynelos lemanensis*, and reveals that the radiation of the Amphicyonini is more complex than has generally been admittted (Morales *et al*. 2021).

Genus *Mogharacyon* nov.

Type species :- *Mogharacyon anubisi* (Morlo *et al*. 2019)

Type locality :- Moghara, Egypt

Age :- Middle Miocene.

Diagnosis:- Medium-sized Amphicyonini (Length m/1 - 26-29 mm); robust mandible with complete premolar series, anterior premolars (p/1-p/2) uniradiculate, reduced in dimensions, short diastemata between p/4-m/1 and p/4-p/3; p/4 relatively large without mesial cuspid, distal cuspid well-developed, talonid slightly broadened; m/1 extremely sectorial, with tall trigonid compressed bucco-lingually, metaconid very reduced, short, narrow talonid dominated by a tall, extended hypoconid, small entoconid; m/2 relatively broad compared to the m/1, with tall trigonid in which the paraconid is reduced, narrow talonid dominated by the hypoconid with reduced entoconid; P4/ with transversely compressed paracone, parastylar area enlarged with small parastyle. The metastyle is broad and is in line mesio-distally with the paracone; the protocone is small and backs onto the mesio-lingual base of the paracone; the flexus is well developed in the mesial wall between the protocone and the base of the parastyle; basal cingulum surrounding the entire tooth; M1/ subtriangular, paracone bigger and taller than the metacone, the two cuspids are tall, the parastyle and metastyle very small, moderate buccal cingulum; small paraconule and metaconule; the lingual part of the molar is clearly reduced with a well-developed duniform protocone which is displaced mesially; prominent lingual cingulum surrounding the base of the protocone that is strongly developed linguo-distally; large M2/.

Species *Mogharacyon anubisi* (Morlo *et al.* 2019)

Synonymy :-

2007 *Cynelos* nov. sp. Morlo *et al.* p. 149-151.
2010 *Hecubides* sp. Morales *et al*. p. 48.
2010 *Cynelos* sp. Werdelin & Peigné, p. 604.
2016 *Afrocyon* nov. sp. Morales *et al*. p. 143.
2019 *Cynelos anubisi* nov. sp. Morlo *et al.* p. 734.
2019 *Amphicyon giganteus*, partim, Morlo *et al*. p. 738.

Holotype :- CUWM 55, left mandible with alveolus of c/1, single root of p/1, single root of p/2, roots of p/3, p/4-m/2, and alveolus of m/3 (Morlo *et al*. 2019).

Other material :- DPC 14532/1 from Moghara L-7, isolated left P4/; DPC 8981 from Moghara L-7, isolated left M2/; DPC 14532/2 from Moghara L-7, isolated left m/1; DPC 5426 from unknown locality at Moghara, isolated left M1/ (Morlo *et al*. 2007, Fig. 4).

Type locality :- Moghara, Egypt

Age :- Late early Miocene (known only from Moghara) contemporaneous with European biozone MN4.

Diagnosis :- As for the genus.

Discussion

Morlo *et al*. (2019) having accepted the use of the name *Cynelos* recently proposed a new species *Cynelos anubisi* based on specimens from Moghara, Egypt. The dimensions of the p/4-m/2 of the holotype (mandible CUWM 55) are intermediate between the holotype of *Afrocyon burolleti* Arambourg, 1961, and the mandible NHMUK M 82373, also from Gebel Zelten, attributed to this same species by Morales *et al.* (2010) and that Morlo *et al*. (2019) identified as cf. *Amphicyon* or *Amphicyon* sp. Morphologically, the dentition of the holotype of *C. anubisi* is quite close to that of *Namibiocyon ginsburgi*; the p/4 has a slightly widened talonid, the m/1 is sectorial with a narrow talonid almost completely occupied by the hypoconid, and the same applies to the m/2. In these features, it differs from *Afrocyon burolleti* (including the mandible NHMUK M 82373). However, it differs from *Namibiocyon ginsburgi* by the greater robusticity of its mandibular corpus, the greater reduction of the anterior premolars, in which the p/2 is uniradiculate and the greater size of the p/4 and m/2 relative to m/1, as well as the more sectorial morphology of the m/1 (Morlo *et al*. 2019) (Figs 1-2, 4-5).

In our opinion these characters do not permit the mandible CUWM 55 to be attributed to the genus *Namibiocyon*, and furthermore they distance it from both *Cynelos lemanenis* and *Afrocyon burolleti*, leading us to erect a new genus for the form from Moghara, which we name *Mogharacyon* nov. gen. *anubisi* (Morlo *et al*. 2019).

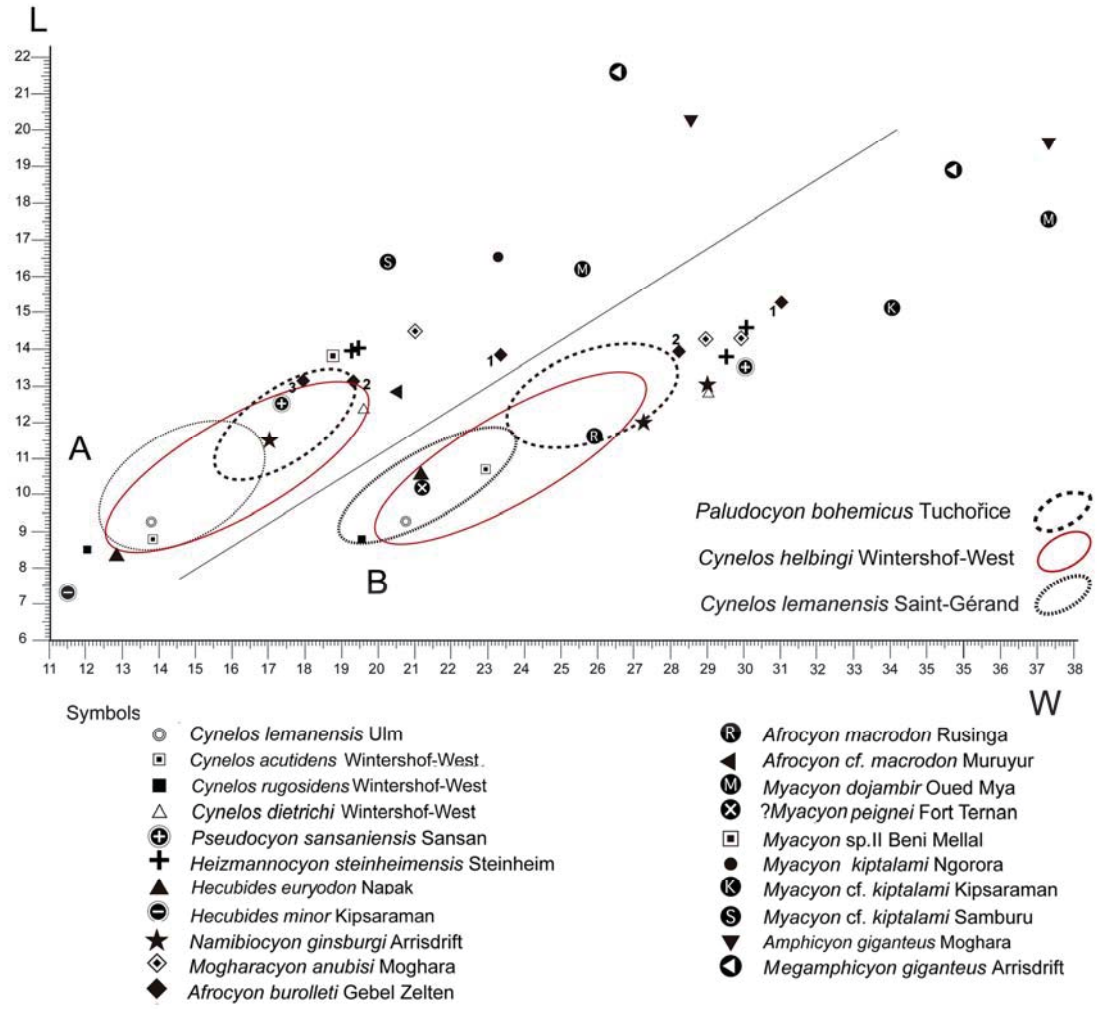

Figure 1. Bivariate plots of length and width of the lower dentition (m/1-m/2) of selected European small and medium-sized Amphicyoninae compared with the African species. A) m/1; B) m/2. Data from Dehm (1950), Ginsburg (1961, 1977a,b); Peigné (2012), Heizmann (1973), Morales *et al*. (1998, 2003, 2007, 2010, 2016) Morales & Pickford (2008); Morlo *et al*. (2019); Peigné (2012), Peigné & Heizmann (2003), Sudre & Hartenberger (1992); Tsujikawa (2005) and Werdelin (2020). Ellipses: Outline with large dots, teeth range of *Paludocyon bohemicus* from Tuchořice. Continuous outline, teeth range of *Cynelos helbingi* from Wintershof-West. Outline with small dots, teeth range of *Cynelos lemanenis* from Saint Gérand le Puy. Abbreviations: L, length. W, width.

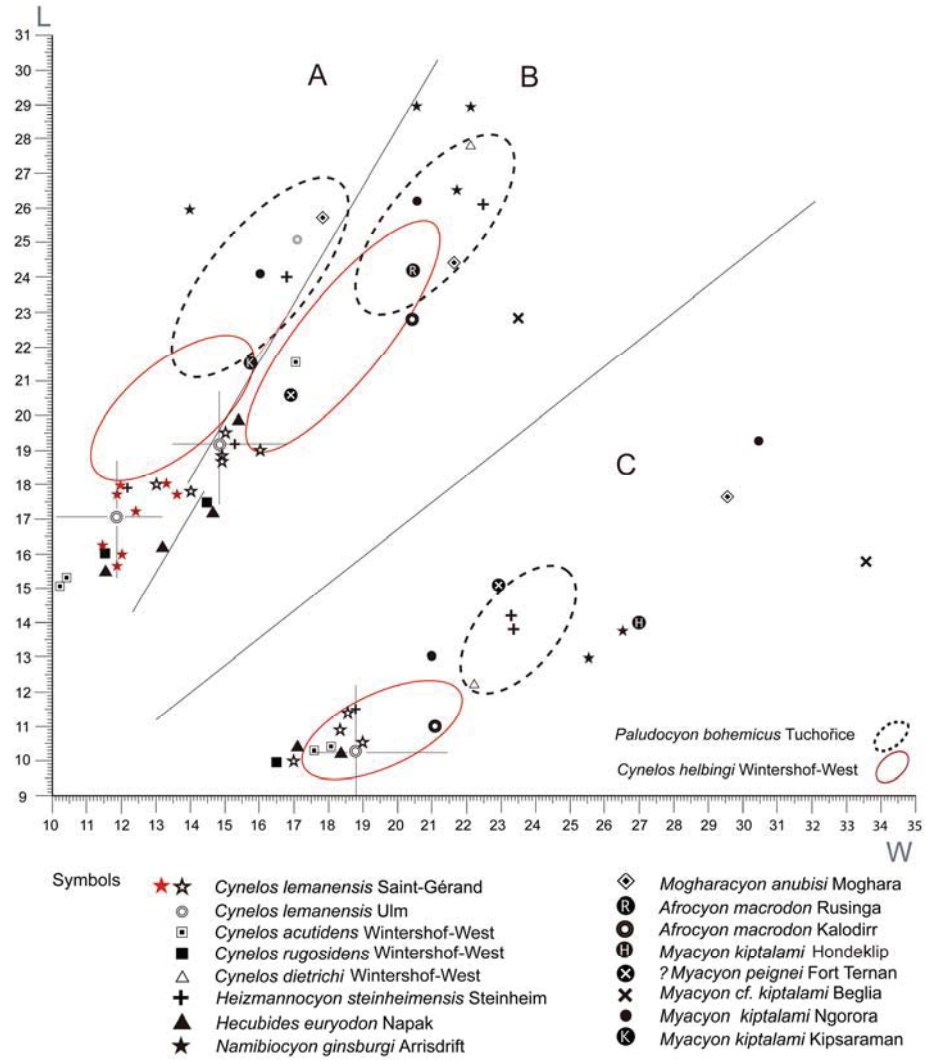

Figure 2. Bivariate plots of length and width of the upper dentition (P4/, M1/ and M2/) of selected European small and medium-sized Amphicyoninae compared with the African species. A) M2/; B) M1/; C) P4/. Data from Adrian *et al*. (2018); Dehm (1950); Ginsburg (1977a); Heizmann (1973); Kurtén (1976); Morales *et al*. (1998, 2003, 2007, 2016); Morales & Pickford (2005, 2008); Morlo *et al*. (2019); Werdelin (2020). Continuous line: ranges of maximum and minimum values from the average of teeth of *Cynelos lemanensis* from Ulm, Germany (Peigné & Heizmann 2003). Red open star M2/, Black open star M1/ of *Cynelos lemanensis* from Saint Gérand le Puy. Ellipses: Outline with large dots, teeth range of *Paludocyon bohemicus* from Tuchořice. Continuous outline, teeth range of *Cynelos helbingi* from Wintershof-West. Abbreviations: L, length. W, width.

Inclusion of their new species in the genus *Cynelos* by Morlo *et al*. (2007) probably had an influence on the attribution of the other four specimens from Moghara. Out of the fossils identified as *Cynelos* nov. sp., only the m/1 (DPC 14532/2) that is morphologically similar to the corresponding tooth in the holotype, can be retained in the species *Cynelos anubisi*. In contrast, the other three teeth - left P4/ (DPC 14532/1), left M1/ (DPC 5426), left M2/ (DPC 8981) – corresponding to the upper dentition, possess morphology that distances them from *C. lemanensis* and were included by Morlo *et al*. (2019) in the large form described from the same locality as *Amphicyon giganteus*. In our opinion these three teeth should be included in *Mogharacyon anubisi*; the M1/ is of slightly smaller dimensions than the holotype of *Namibiocyon ginsburgi*, but its morphological features, with very tall buccal cusps and shortened lingual part correlate well with the m/1 in the holotype mandible of the species, as well as the isolated m/1 (DPC 14532/2) also attributed to this taxon. The same applies to the P4/ which possesses a broadened metastyle corresponding to the

elongation of the trigonid of the m/1. It is also expected that the large m/2, as in the holotype of *"C." anubisi*, corresponds to an unreduced M2/ as in DPC 8981. The inclusion of this upper dentition in *Mogharacyon anubisi* accentuates the distinctiveness of the Egyptian species from *Cynelos lemanensis*.

The proportions of the lower dentition of *Mogharacyon anubisi* are close to those of *Afrocyon burolleti* (Fig. 1) the two species sharing the large size of the p/4 and m/2 relative to the m/1, but the species from Moghara has more sectorial m/1 and m/2 than the Libyan species. Reduction of the premolar series reveals that *Mogharacyon anubisi* is, in this character, close to the more hypercarnivorous species of the Thaumastocyoninae, but with the difference that they have retained large second molars, features cited by Morales *et al*. (2016) to discount the presence of *Agnotherium* in the African localities. *Mogharacyon anubisi*, like *Namibiocyon ginsburgi* has well developed hypercarnivorous adaptations, but with divergent characteristics. For example, the m/2 and p/4 are small relative to the m/1 in *N. ginsburgi*, and the m/1, although clearly sectorial, is less so than in *Mogharacyon anubisi*, which, in this morphology is close to *Pseudocyon sansaniensis* from the middle Miocene of Sansan, France (Ginsburg, 1961; Peigné, 2012) or to *Magericyon castellanus* (Ginsburg *et al*. 1981) and *Magericyon anceps* (Peigné *et al*. 2008) from the upper Miocene of Spain.

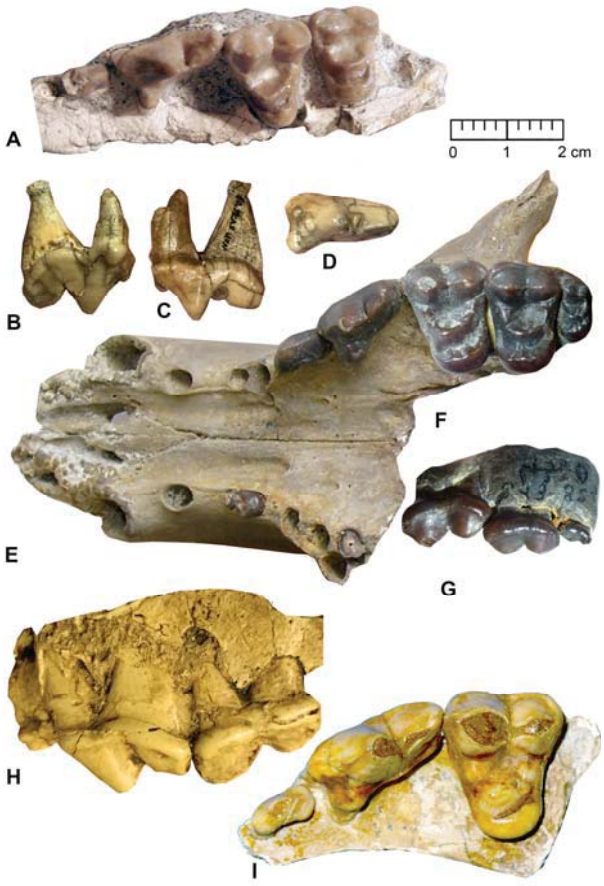

Figure 3. Comparison of the upper dentitions of Amphicyonidae. A-D) *Hecubides euryodon* Savage 1965. A) Left maxilla (part of the holotype NHMUK M 19084) from Napak I, Uganda, in occlusal view; B-D) Left P4/ (UM NAP XV 76'08) from Napak XV, Uganda, B) lingual view. C) buccal view. D) occlusal view. E-G) *Cynelos lemanensis* (Pomel, 1846) from Saint Gérand le Puy. E-F) Composition of the partial skull (FSL 65-655) and maxillary fragment with M3/-M2/ (FSL 213 824) in occlusal view (mirrored). G) Maxilla fragment (FSL 213 824) in buccal view (mirrored). H-I) *Namibiocyon ginsburgi* (Morales *et al*. 1998) from Arrisdrift, Namibia, right maxilla fragment with P3/-M1/ (GSN AD 604'94), H) buccal view, I) occlusal view (mirrored).

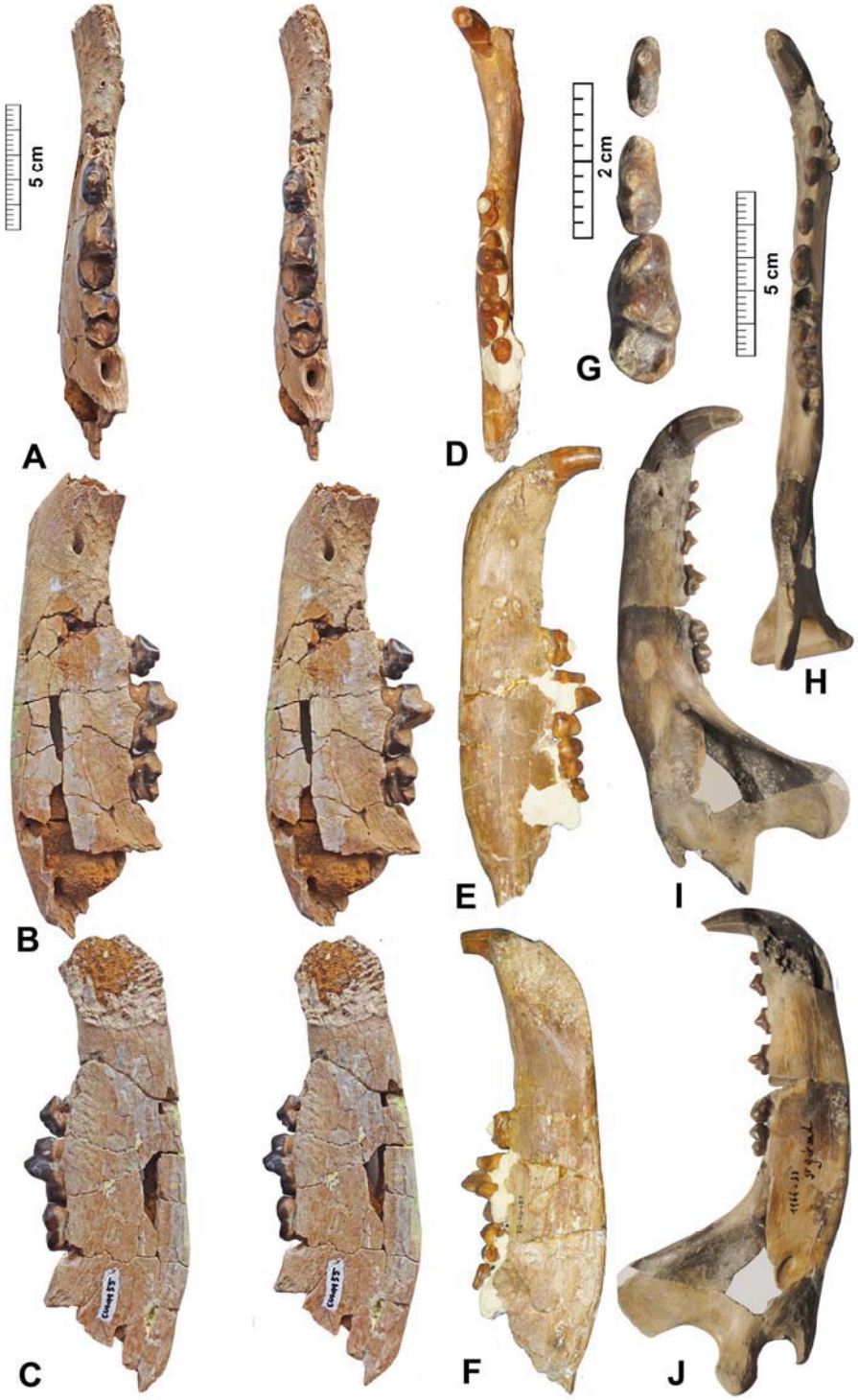

Figure 4. Comparison of the mandibles and lower dentitions of *Mogharacyon anubisi*, *Namibiocyon ginsburgi* and *Cynelos lemanensis*. A-C) *Mogharacyon anubisi* (Morlo *et al*. 2019) from Moghara, Egypt. A) left mandible with p/4-m/2 (CUWM 55). A) occlusal view; B) buccal view; C) lingual view (stereo pairs). D-F) *Namibiocyon ginsburgi* (Morales *et al*. 1998) from Arrisdrift, Namibia, left mandible (GSN PQ AD 133) with c/1 and p/4-m/3, D) occlusal view; E) buccal view; F) lingual view. G-J) *Cynelos lemanensis* (Pomel, 1846) from Saint Gérand le Puy, France. G) p/3-m/1 (MNHN SG 9981) in occlusal view. H-J) left mandible (MNHN SG 490) with c/1-m/2 (m/1 with broken trigonid). H) occlusal view; I) buccal view; J) lingual view.

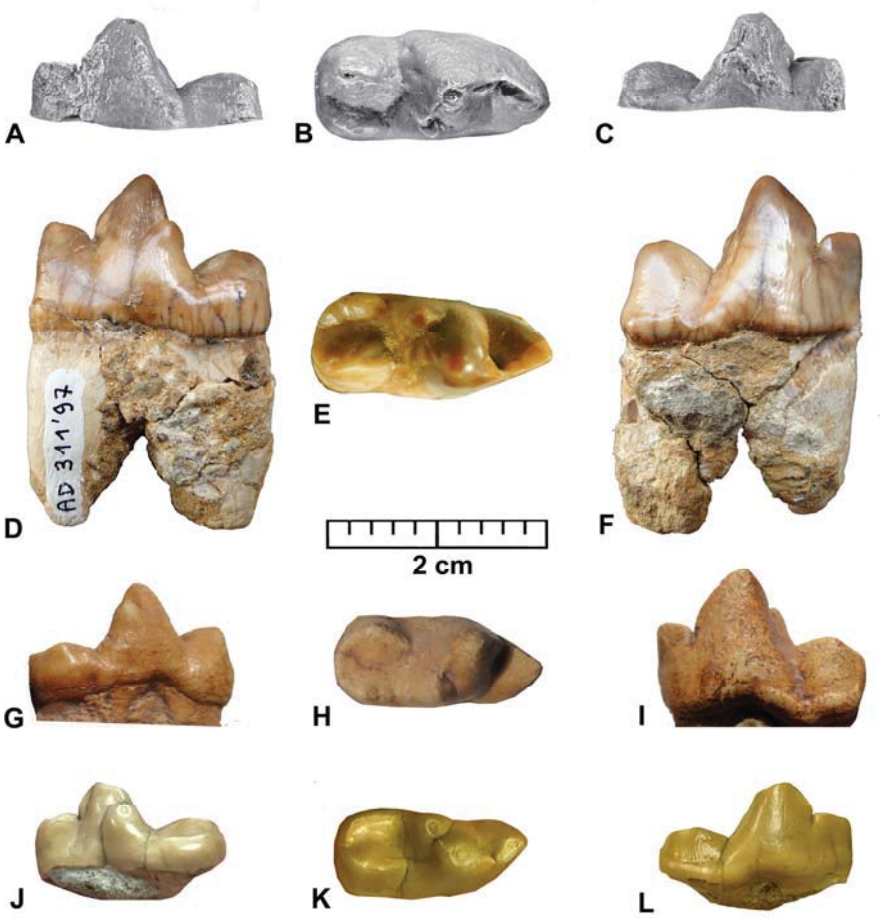

Figure 5. Comparison of the lower carnassial teeth (m/1) of *Mogharacyon anubisi*, *Namibiocyon ginsburgi*, *Cynelos lemanensis* and *Hecubides euryodon*. A-C) *Mogharacyon anubisi* (Morlo *et al*. 2019) from Moghara, Egypt (left m/1 DPC 14532/2 L7 figured in Morlo *et al*. 2007). A) buccal view; B) occlusal view; C) lingual view. D-F) *Namibiocyon ginsburgi* (Morales *et al*. 1998) from Arrisdrift, Namibia (right m/1, GSN AD 311'97). D) lingual view; E) occlusal view; F) buccal view. G-I) *Cynelos lemanensis* (Pomel, 1846) from Saint Gérand le Puy, France (left m/1 Coll. Duligne; Ginsburg, 1977a). G) lingual view; H) occlusal view; I) buccal view. J-L) *Hecubides euryodon* Savage, 1965, from Napak XV, Uganda (right m/1, UM NAP XV 4'12). J) lingual view; K) occlusal view; L) buccal view.

The combination of very sectorial carnassial teeth (m/1-P4/) with unreduced second molars was employed by Morales *et al*. (2016) to validate the genus *Myacyon* Sudre & Hartenberger, 1992, although, as argued by Werdelin (2019) the restricted and damaged nature of the mandible of the type species *Myacyon dojambir* introduced an element of taxonomic instability. We agree with the observations of Werdelin (2019) but at the least, the use of this taxon for the African forms introduces less uncertainty than would maintaining it in the genus *Agnotherium*, a form that is above all poorly known, but in which the m/2 - and by correlation the M2/ - would be very reduced in relation to the m/1 as occurs in other Thaumastocyoninae (Morlo *et al*. 2020).

This renders unlikely the possibility of convergent evolution in the African species, which indubitably present hypercarnivorous adaptations but more moderate than is typical of Thaumastocyoninae (Morales *et al*. 2016, 2019, 2021). *Mogharacyon anubisi* appears to be primitive in the morphology of its P4/, in that the development of the parastylar part is incipient, despite the fact that in forms related to *Myacyon* it is strongly developed as occurs in ?*Myacyon peignei* Werdelin, 2019 - Fort Ternan, Kenya - *Myacyon kiptalami* (Morales & Pickford) 2005 – type locality Ngorora, Kenya, and Hondeklip Bay, South Africa – *Myacyon* cf. *kiptalami* from the Beglia Formation, Tunisia (Kurten, 1976). The m/2 of *Mogharacyon anubisi* is

close in morphology to that of *Myacyon kiptalami* from Ngorora (Morales *et al*. 2010), as are those of the specimens from Samburu, Kenya (Tsujikawa, 2005) and of *Myacyon dojambir* (Sudre & Hartenberger, 1992). In summary, even though knowledge about the forms that occur near the middle/late Miocene boundary is restricted, the available data indicate a possible phylogenetic relationship between *Mogharacyon anubisi* and the forms included in *Myacyon*.

Conclusions

Until its resurrection by Kuss (1965a), the genus *Cynelo*s Jourdan 1862, was largely forgotten, the species attributed by the German author to *C. lemanensis* (Pomel, 1846), and *C. rugosidens* (Schlosser, 1899), having been included in *Amphicyon* Lartet, 1839. In fact Beaumont, 1962, wrote that "*Le genre* Amphicyon*, tel qu'il est conçu actuellement, n'est qu'un nom qui masque une méconnaissance preque totale des formes qu'il renferme, de leurs rapports entre elles et des origines*". Since the publication by Kuss (1965a) the quantity of species attributed to the genus has increased notably, eventually including species from the Oligocene - *Cynelos piveteaui* Ginsburg, 1966 and *Cynelos crassidens* (Filhol) 1876 (= *Cynelos rugosidens vireti* Kuss, 1965b; see Ginsburg, 1966) – as well as species from the end of the middle Miocene. The problems highlighted by Beaumont (1962) concerning *Amphicyon*, some species of which have been transferred to *Cynelos*, mean that a profound revision of the genus is required.

The presence of *Cynelos* in Africa is debatable, and in any case is dependent on the taxonomic status of *Hecubides*. The two genera share numerous characters which support their inclusion in the same tribe Amphicyonini. Several species of European *Cynelos* are well represented, as for example the type species *Cynelos lemanensis* from Saint Gérand le Puy, France (Viret, 1929; Ginsburg, 1977a), which is also abundant at Ulm, Germany (Peigné & Heizmann, 2003). For this reason, our comparisons have been focussed on this species, and not on the plethora of other species included in the genus. Otherwise a general revision of the genus would be required, some species clearly sharing characters with *Cynelos lemanensis*, at the same time as showing species differences, as in the case of the species from North America recently described by Hunt & Stapleton (2014) and Hunt & Yatkola (2020). But this is not the case with some other species such as *Cynelos schlosseri*, *Cynelos bohemicus*, *Cynelos steinheimensis* and possibly others (Ginsburg, 1999; Morales *et al*. 2021). In our opinion, the same applies to *Hecubides euryodon* which differs from *Cynelos lemanensis* in the morphology of the upper molars, in that the M1/ is not lingually widened, conserving a subtriangular morphology, in that the lingual part included in the cingulum is weakly developed, the buccal cusplets of M1/ are taller; the P4/ is more gracile and in the lower dentition, the m/2 and m/3 are more reduced. These characters reveal a clear divergence between the forms, which certainly needs to be analysed within a broader context, but which is beyond the scope of the present paper.

Considering all the evidence, it is concluded that the younger species from Arrisdrift and Moghara have reached a level of divergence from the more ancient lineages of *Cynelos lemanensis* and *Hecubides euryodon* that indicates that classifying all of them within a single genus is no longer realistic, and for this reason we propose new genus names for the two younger species.

Evidently there remain several problems to resolve concerning the systematics of the family, and these are exacerbated among those African representatives which are poorly known or poorly preserved.

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