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Brief report

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A new genus of "miacid" carnivoran from the earliest Eocene of Europe and North America

THIERRY SMITH and RICHARD SMITH

"Miacid" carnivorans comprise one of the modern mammal groups appearing around the Palaeocene–Eocene Thermal Maximum (PETM) in the Northern Hemisphere. Here we describe a new very small "miacid" carnivoran from the earliest Eocene of Dormaal, Belgium, that shares a particular dental morphology with the species "*Miacis*" *winkleri* and "*Miacis*" *rosei* from the early Eocene of North America. The three species present very gracile and sharp teeth, and are hereby placed in the new genus *Gracilocyon*. Comparative dental analysis of *Gracilocyon* with other early "miacids" contributes to better resolve the polarity of dental characters and indicates that this genus is one of the most primitive members of the family. Diversity of early modern carnivorans is greater than previously considered and early "miacids" seem to have dispersed into North America from two different geographic origins.

Introduction

Carnivorans of modern aspect are represented by the crown group Carnivora plus the stem family "Miacidae", all possessing derived features such as a rounded infraorbital foramen, a rostral entotympanic and a deep fossa for the tensor tympani muscle in the middle ear; these characters are absent in viverravid carnivorans (Wesley-Hunt and Flynn 2005; Polly et al. 2006). Modern carnivorans make their first occurrence in the fossil record during the earliest Eocene on the three continents of the Northern Hemisphere. One exception seems to be the species *Uintacyon rudis* that appears a little earlier, in the latest Palaeocene of Wyoming, USA (Cf-2,3, middle–late Clarkforkian North American Land Mammal Age [NALMA], Gingerich 1983). The early Eocene modern carnivorans all belong to the well-known family "Miacidae" that is considered as paraphyletic because its members are united by their lack of the diagnostic features recognised in later carnivoran clades (Wesley-Hunt and Flynn 2005). This unclear evolutionary pattern is also due to the fact that the genus "*Miacis*" has been a wastebasket taxon for long time (Wang and Tedford 1994), that the direct ancestors of "miacids" are unknown, and that the polarity of characters in this basal group is unresolve.

The earliest Eocene locality of Dormaal, Belgium, which is the reference-level MP7 of the mammalian biochronological scale for the European Palaeogene, has already yielded several basal taxa that apparently lie close to the origin of modern groups from North America (Smith et al. 1996; Smith and Smith 2001; Smith et al. 2006). Here we describe a new genus of a very small and primitive "miacid" carnivoran that is present in Dormaal and other early Eocene localities of northwestern Europe and in the early Eocene of Wyoming (Wa-0 to Wa-2, early Wasatchian NALMA). It shows characters that are quite distinct from those of other "miacid" genera, indicating higher morphological diversity among basal "miacids" than previously thought.

Institutional abbreviations.—IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; UCMP, University of California Museum of Paleontology, Berkeley, USA; UM(VP), University of Michigan (Vertebrate Paleontology), Ann Arbor, USA; YPM, Yale Peabody Museum-Princeton Collection, New Haven, USA.

Other abbreviations.—D (Dormaal), TS (T. Smith), WL (Wouters-Lepage), Dormaal, general collections of the IRSNB; DIICRS, DIIIRS, Dormaal, collection R. Smith (corresponding to the layers mentioned in Smith and Smith 1996); DMG, Dormaal, collection R. Smith (old collection Michel Girardot); Eq, Erquelinnes, general collections of the IRSNB; NALMA, North American Land Mammal Age.

Systematic palaeontology

Order Carnivora Bowdich, 1821

Family "Miacidae" Cope, 1880

Genus *Gracilocyon* nov.

Figs. 1, 2.

Type species: *Miacis winkleri* (Gingerich, 1983) comb. nov.

Etymology: From Latin *gracilis*, gracile, slender; from Greek *kyon*, dog.

Included species: *Gracilocyon winkleri* (Gingerich, 1983), *G. rosei* (Heinrich, Strait, and Houde, 2008) comb. nov., and *G. solei* sp. nov.

Diagnosis.—Small "miacid" differing from all other "miacid" genera by a gracile and sharp dentition; narrow lower premolars with salient paraconid on p3–4; posterior accessory cusp present on p4 talonid; high crowned p4 and m1–2; three lower molars with long talonid basin; M1 with triangular outline, nearly symmetrical stylar shelf with long and labially oriented postmetacrista, deep ectoflexus, and antero-posteriorly short protocone; M2 short and wide with well developed stylar shelf.

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Gracilocyon solei sp. nov.

Fig. 1, Table 1.

Etymology: Named for Floréal Solé in recognition of his contribution to the understanding of the early Eocene carnivorans.

Holotype: IRSNB M1327 (DIII314RS), left M1.

Type locality: Dormaal, Flemish Brabant, Belgium (Smith and Smith 1996).

Type horizon: Dormaal Member, Tienen Formation, Landen Group, earliest Eocene, reference level MP 7 (see Aguilar et al. 1997).

Referred material.—DIIC254RS, right p4; IRSNB M1325 (TS46), right p4; Eq18, right p4; IRSNB M1326 (D133), left m2; TS62, left m2; DIIC1718RS, left M1; WL1422, right M2; IRSNB M1328 (DIII795RS), left M2; DIII2163RS, left M2; D2462MG, left M2.

Differential diagnosis.—*Gracilocyon solei* gen. et sp. nov. differs from all the members of the "Miacidae" except *G. rosei* by its very small size. Differs from *G. winkleri* by the deeper talonid basin on p4 and m2, and a more lingual paraconid and a narrower talonid basin on m2. Differs from *G. rosei* by the deeper ectoflexus and the larger and more labially placed metastylar lobe on M1.

Geographic and stratigraphic range.—*Gracilocyon solei* is known from the earliest Eocene (MP7) Tienen Formation at Dormaal (Flemish Brabant) and Erquelinnes (Hainaut) in Belgium.

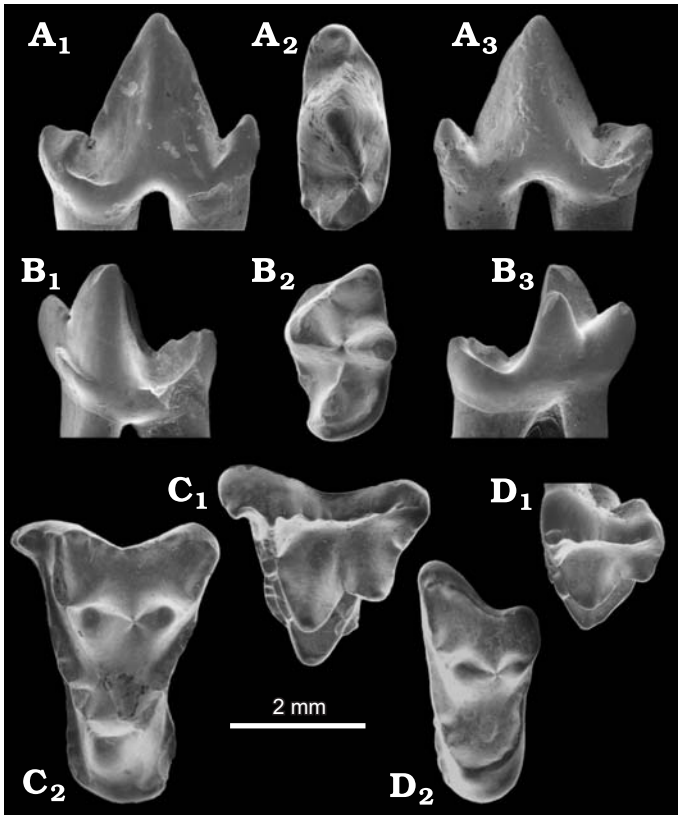


Fig. 1. "Miacid" carnivoran *Gracilocyon solei* sp. nov., from the earliest Eocene of the Tienen Formation, Dormaal, Belgium, in labial (A_1–D_1), occlusal (A_2–D_2), and lingual (A_3, B_3) views. **A**. IRSNB M 1325 (TS46), Rp4. **B**. IRSNB M 1326 (D133), Lm2. **C**. IRSNB M 1327 (DIII314RS, holotype), LM1. **D**. IRSNB M 1328 (DIII795RS), LM2. SEM micrographs.

Table 1. Measurements in mm of the lower and upper teeth of *Gracilocyon solei* sp. nov.

Tooth	Number	Length	Width
p4	DII254S	3.4	1.4
	IRSNB M 1325	3.2	1.3
	Eq18	–	1.4
m2	IRSNB M 1326	2.6	1.6
	TS62	2.6	1.7
M1	IRSNB M 1327	3.1	4.4
	DIIC1718RS	3.4	4.7
M2	WL1422	2.1	3.9
	IRSNB M 1328	1.9	3.6
	DIII2163RS	2.1	3.9
	D2462MG	2.1	3.7

Description

The p4 presents a well individualised and high paraconid. The high, narrow and slender protoconid has a central position on the crown. Trigonid and talonid are approximately equal in width.

The m2 has a moderately high trigonid. Protoconid and metaconid are close to each other, delimiting a narrow trigonid basin. The metaconid is higher than the paraconid. The cristid obliqua presents a swelling at its posterior part (vestigial hypoconid?). The talonid is as long as the trigonid. The talonid basin is long and narrow and presents a small median posterior cusp at its extremity (vestigial hypoconulid?).

M1 is short and wide. Paracone and metacone are close to each other. The metacone is distinctly lower than the paracone. The slender postmetacrista is labially oriented and nearly as long as the preparacrista forming a nearly symmetrical stylar shelf. The ectoflexus is deep. Paraconule and metaconule are present and well developed. The paraconule presents a postparaconule crista joining the base of the paracone. The protocone is short anteroposteriorly and surrounded by pre- and postcingulum.

M2 has a long parastylar lobe. An ectoflexus is present. The paracone is salient. The preparacrista is slender as in M1. A paraconule is present with a discrete postparaconule crista. The protocone has about the same length as in M1 but is less wide. A small precingulum is present but there is no postcingulum.

Discussion

The new species from the earliest Eocene of Belgium is closely related to the North American species "*Miacis*" *winkleri* from the early Wasatchian (Wa-0 to 2) of Park County, Wyoming, as documented by the following features: small size, gracile aspect of the teeth, unreduced m2 with a high trigonid and a narrow deep talonid, shearing and high p4 with a salient paraconid. Nevertheless, the holotype of the small "*Miacis*" *winkleri* (UM75438, Wa-2) is still 27 % larger than the tiny Belgian species, and the talonid basin of m2 is somewhat proportionally wider and shallower. The Belgian species also appears to be closely related to "*Miacis*" *rosei* from the early Wasatchian (Wa-0) of Washakie County, Wyoming: M1 (UCMP 216045) of "*M.*" *rosei* has exactly the same size and also presents a wide stylar shelf with deep ectoflexus, together with weakly developed cingula around an

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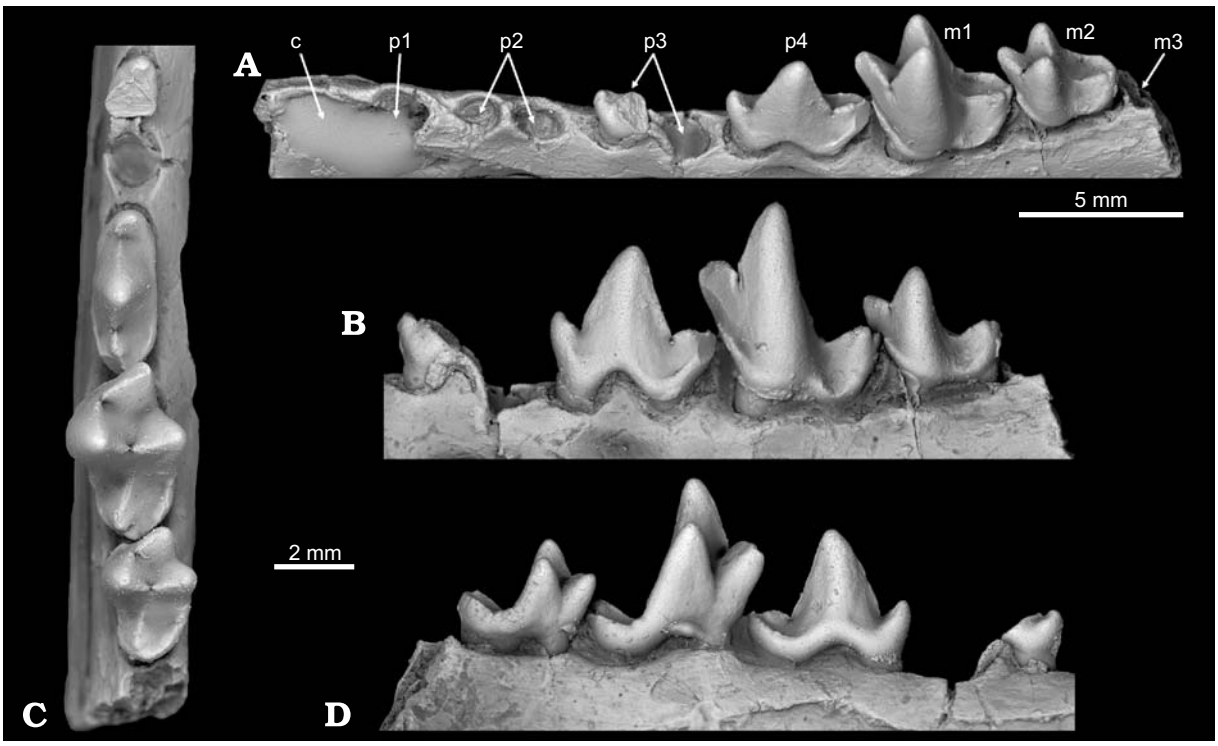


Fig. 2. "Miacid" carnivoran *Gracilocyon winkleri* (Gingerich, 1983) comb. nov., from the early Eocene of the Willwood formation, locality Sc-210 (Wa-2), Clark's Fork basin, Wyoming, USA, UM 75432 (holotype). Left dentary with p4–m2 in oblique labial (**A**), labial (**B**), occlusal (**C**), and lingual (**D**) views.

antero-posteriorly short protocone. The differences lie in the shallower ectoflexus and the metastylar lobe that projects less labially in the M1 of "*Miacis*" *rosei*, the latter character being derived (Wesley-Hunt and Flynn 2005) and probably indicating a reduction in width of the M2, as usual in "miacids". The discovery of isolated lower and upper teeth of the Belgian species, combined with associated lower teeth of "*M.*" *winkleri* and one isolated upper tooth of "*M.*" *rosei*, permits the three species to be grouped in the new genus *Gracilocyon*. In addition to features already mentioned, *Gracilocyon* is also characterised by the paracone higher than metacone on M1, and by high trigonid on m1. These characters indicate that *Gracilocyon* belongs to the classical family "Miacidae" and presents a basal position by the retention of many plesiomorphic characters.

By its diagnostic characters, *Gracilocyon* is clearly distinct from other "miacid" genera (*Miacis*, *Palaearctonyx*, *Procynodictis*, *Prodaphaenus*, *Tapocyon*, *Uintacyon*, *Vassacyon*, *Vulpavus*, *Prohesperocyon*, *Paramiacis*, *Paroodectes*, *Messelogale*, *Quercygale*, *Chailicyon*, *Xinyuictis*). The only exception, a possible relative of *Gracilocyon*, is the North American genus *Oodectes*. The latter is generally considered as one of the most primitive "miacid" in the phylogenetic analyses of early carnivorans (Wesley-Hunt and Flynn 2005). *O. herpestoides* Wortman, 1901 from the Bridgerian and *O. jepseni* (Guthrie, 1967) from the late Wasatchian are ge

ologically much younger than *Gracilocyon* and have about the same size as *G. winkleri*. Like *Gracilocyon*, *Oodectes* retains many plesiomorphic characters. They share the deep ectoflexus on upper molars, the long para- and metacrista, the discontinuous cingulum around the protocone of the upper molars, and the long and high lower premolars. However, *Oodectes* differs from *Gracilocyon* by several apomorphies, such as the reduction or absence of the paraconid on p3 and p4, the presence of a well-developed and complete lingual cingulid on p4, the antero-posterior shortening of the talonid on the last premolars and molars, and a more developed lingual cingulum on M2 (visible on YPM 11861).

The cladistic analysis of Heinrich (1997), based on the study of the oldest North American "miacid" genera, indicated that equal para- and metastylar lobes on upper molars is a derived character. In absence of upper teeth of *G. winkleri*, Heinrich selected the upper molars of *Miacis deutschi* to represent the primitive condition. In contrast, based on the study of a complete skull of *Oodectes herpestoides*, Wesley-Hunt and Flynn (2005) considered an equal or subequal projection of the parastylar and metastylar lobe on M1 as the primitive condition in "miacids". The discovery of upper teeth of the primitive *Gracilocyon*, with morphology similar to that of *Oodectes*, supports the hypothesis of Wesley-Hunt and Flynn (2005). The metastylar lobe seems thus to have been labially projected, nearly as the parastylar lobe, in basal carnivorans. We presume that this metastylar lobe became reduced in several genera including *Miacis*. This was probably in parallel with the reduction in width of the M2. However, other genera such as *Vulpavus* apparently developed another type of mastication that emphasised crushing. In *Vulpavus*, the metastylar lobe of M1 would not have been reduced but the postmetacrista disappeared, the P4 did not really develop but the talonid of the lower molars became larger.

The general dental morphology of *Gracilocyon* is reminiscent of that of *Cimolestes*, supporting the hypothesis discussed

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by several authors (Mac Intyre 1966; Lillegraven 1969; Fox and Youzwyshyn 1994) that the ancestor of carnivorans was related to cimolestid (didelphodontan) mammals. It is also remarkable how much the m1 and M1 of the carnivoran *Gracilocyon* are similar to the m2 and M2 of the basal hyaenodontid creodont *Prototomus*. The dental similarities between the primitive "miacid" *Gracilocyon* and these other primitive members of Ferae add precision to the determination of polarities of some dental characters among early carnivorans. Moreover, the morphology of p4, m1, and M1 suggests that the P4/m1 carnassial pair of *Gracilocyon* was probably weakly developed.

Among the early Wasatchian "miacid" species, *G. winkleri*, *Miacis deutschi*, and *M. exiguus* were believed to belong to the same lineage (Gingerich 1983). These three species are indeed present in successive horizons of the Clark's Fork Basin. Based on new "miacid" species described from the Wa-0 of Wyoming, Heinrich et al. (2008) recently suggested that the family "Miacidae" had diversified to a greater extent by the Palaeocene–Eocene boundary than previously recognised. These authors recognised at least four lineages, *Uintacyon*, *Miacis*, *Vassacyon*, and *Xinyuictis*, as well as a fifth, enigmatic lineage represented by *Oodectes*. The seeming absence of *Uintacyon* in Europe and its early (late Clarkforkian) presence in North America suggest that this genus may have immigrated from Asia via the Bering Bridge.

The MP7 "miacid" carnivorans of Dormaal are represented by two or three species. *Miacis latouri* Quinet, 1966 and another somewhat larger form at Dormaal are close to *M. deutschi* (Smith 1999), whereas *G. solei* is closely related to *G. rosei* and *G. winkleri*. The presence of *Gracilocyon* and *Miacis* already in the earliest Eocene of Dormaal, with very primitive aspect and very small size, suggest that these two genera were present in Europe before dispersing to North America. A similar migration route (via the Greenland Bridge) has been already suggested for the primate *Teilhardina*, the artiodactyl *Diacodexis* and the hyaenodontid creodonts *Arfia*, *Prototomus*, and *Galecyon* (Smith et al. 1996; Smith and Smith 2001; Smith et al. 2006), five genera of three additional modern mammal orders that appeared around the PETM in the Northern hemisphere. In the case of *Teilhardina* the genus could have originated in south Asia (Smith et al. 2006). However, some hyaenodontid creodonts may have originated in North Africa (Gheerbrant et al. 2006; Solé et al. 2009).

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