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The “miacids” (Carnivoraformes, Mammalia) from the Early Eocene locality of Le Quesnoy (MP7, France); first occurrence of *Vassacyon* in Europe*Les « miacidés » (Carnivoraformes, Mammalia) du Quesnoy (Éocène inférieur, MP7, France); première occurrence du genre Vassacyon en Europe*Floréal Solé^{a,b,*}, Emmanuel Gheerbrant^a, Marc Godinot^a^a CNRS (E.G.) and EPHE (M.G.), UMR 7207 CR2P, Muséum national d'histoire naturelle, département « Histoire de la Terre », CP 38, CNRS, Centre de recherche sur la paléobiodiversité et les paléoenvironnements, 57, rue Cuvier, 75005 Paris, France^b Department of Palaeontology, Royal Belgian Institute of Natural Sciences, 29, rue Vautier, 1000 Brussels, Belgium

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ABSTRACT

We describe here “miacid” taxa from the Early Eocene Paris Basin locality of Le Quesnoy (Oise, France). We describe the new species *Vassacyon taxidiotis*, the first European record of this genus. The other “miacids” identified from Le Quesnoy are *Miacis latouri* and *Gracilocyon solei*. The P4 of *G. solei* is described here for the first time. Its morphology (e.g., wide protocone, short postmetacrista) supports a close relationship with *Miacis rundlei* from Abbey Wood (MP8 +9, England). The latter species is therefore classified as *Gracilocyon rundlei*. Three new tooth positions are known for *Miacis latouri*: P4, p4 and m2. They support its reference to *Miacis*. These specimens imply that the European species is more basal than the North American species. The fauna from Le Quesnoy shares with Dormaal the presence of *Miacis latouri* and *Gracilocyon solei*, but the “miacid” fauna from Le Quesnoy also contains *Vassacyon taxidiotis*. The presence in Le Quesnoy of the two former taxa supports a reference to MP7 level of the French locality. The presence of three distinct genera in European localities show that the “Miacidae” were diversified in Europe, as previously observed in North America. The genera *Gracilocyon*, *Miacis*, and *Vassacyon* probably dispersed from Europe to North America during the Palaeocene/Eocene boundary.

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RÉSUMÉ

Nous décrivons dans cet article les « miacidés » de la localité du Quesnoy (Oise, France). Cette dernière est située dans le Bassin de Paris et est datée de l'Éocène inférieur. Une nouvelle espèce de *Vassacyon* est décrite. *Vassacyon taxidiotis* est la première espèce du genre connue en Europe. Les autres fossiles de « miacidés » sont référés à *Miacis latouri* et *Gracilocyon solei*. Une nouvelle position est connue pour *G. solei* : la P4. La morphologie de cette dent est en faveur d'une relation de parenté avec l'espèce *Miacis rundlei* présente à Abbey Wood (MP8 +9, Angleterre). Cette dernière espèce est donc référée au genre *Gracilocyon*. Trois nouvelles positions sont connues pour *M. latouri* : P4, p4 and m2. Elles corroborent la référence du taxon à *Miacis*. La forme européenne apparaît légèrement plus primitive que les formes nord-américaines. La faune du Quesnoy partage avec Dormaal les espèces *M. latouri* et *G. solei*. La présence au Quesnoy de ces deux espèces plaide pour un âge proche

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de celui de Dormaal (MP7) pour la localité française. Cependant, la faune du Quesnoy se démarque par la présence de *V. taxidiotis*. La présence de trois genres de « miacidés » en Europe montre que ce groupe était aussi diversifié en Europe qu'en Amérique du Nord. Les genres *Gracilocyon*, *Miacis*, et *Vassacyon* se sont probablement dispersés d'Europe en Amérique du Nord, lors de la transition Paléocène–Éocène.

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1. Introduction

The systematics of the extinct carnivoramorphans (Viverravidae and Miacidae) has been recently improved by phylogenetic analysis (Spaulding and Flynn, 2012; Wesley-Hunt and Flynn, 2005). The group formed by the crown group Carnivora plus the stem family Miacidae is now termed Carnivoraformes (Flynn et al., 2010). However, the family Miacidae is considered paraphyletic because its members are only united by a lack of the diagnostic features of carnivorans (Wesley-Hunt and Flynn, 2005).

The “Miacidae”, which represent one of the oldest families of Carnivoramorpha (Flynn and Wesley-Hunt, 2005; Flynn et al., 2010), are known since the Late Palaeocene in North America (Gingerich, 1983) and since the Early Eocene over the entire continent of Laurasia (Quinet, 1966; Smith and Smith, 2010; Tong and Wang, 2006). The “Miacidae” differ from the Viverravidae, which are the oldest carnivoramorphan currently known (Fox and Youzwyshyn, 1994) by the presence of m3 and M3. The only known Late Palaeocene “miacid” is *Uintacyon rudis* from the Clarkforkian of North America (Gingerich, 1983; Rose, 1981).

The specialized carnivorous mammals (Hyaenodontidae, Oxyaenidae, Carnivoramorpha) appeared in Europe right after the Palaeocene/Eocene boundary (P/E boundary) (Smith and Smith, 2001, 2010; Solé et al., 2011). In contrast to their poor Late Palaeocene diversity, the “Miacidae” diversified right after the Palaeocene/Eocene boundary in Europe, North America and Asia (Chow, 1975; Gingerich, 1983; Heinrich et al., 2008; Quinet, 1966; Smith and Smith, 2010; Tong and Wang, 2006). Two “miacid” species are known in the MP7 level of Europe: *Miacis latouri* Quinet, 1966, which is considered one of the oldest *Miacis* species (Gingerich, 1983), and *Gracilocyon solei* Smith and Smith, 2010.

The “miacid” fossils described in this article come from the locality of Le Quesnoy (Oise), in the Paris Basin near Houdancourt (Creil area) (Nel et al., 1999), one of the richest localities known from the Early Eocene of Europe. It provides information about the environment, the flora, and the arthropod and vertebrate faunas, and it is important for understanding the mammalian fauna of the Earliest Eocene in Europe. Nel et al. (1999) identified 24 species of mammals representing 20 families. The mammalian fauna appears well diversified and shares a large number of taxa with the Dormaal assemblage. The large species are better represented in Le Quesnoy than in Dormaal, because the French locality is less taphonomically biased. Among the carnivorous fauna, Solé et al. (2011) previously reported the presence of the oxyaenids *Oxyaena woutersi* and *Palaeonictis gigantea* in Le Quesnoy.

2. Material and methods

2.1. Material from Le Quesnoy

The fossils were collected in 1997 and 1998 from two different channels (numbered QNY1 and QNY2). The second channel (QNY2) yielded most of the vertebrate material. All the material is housed in the collection of the Muséum national d'histoire naturelle of Paris.

2.2. Terminology and measurements

Terminology of the molar dental cusps and crests follows Van Valen (1966). The terminology of Ginsburg (1999) is used to describe the premolars. Instead of the term “metastyle”, we use the term “postmetacrista”, which is more adequate functionally. We compared the fossils from Le Quesnoy with casts of the North American and other European “miacids”. The measurements (in mm) follow those used by Gingerich (1983) for “miacids”. The statistical parameters provided are only the observed range (OR) and the mean (M) (Tables 1–3).

Abbreviations

MNHN: Muséum national d'histoire naturelle (Paris, France); IRSNB: Institut royal des sciences naturelles de Belgique (Brussels, Belgium); L: left; R: right; OR: observed range; M: mean.

3. Systematic palaeontology

CARNIVORAMORPHA Wyss and Flynn, 1993

CARNIVORAFORMES Flynn et al., 2010

Table 1

Measurements (in mm) of the specimens of *Gracilocyon solei* Smith and Smith, 2010 from Le Quesnoy (MP7, France).

Tableau 1

Mesures (en mm) des spécimens de *Gracilocyon solei* Smith and Smith, 2010 trouvés au Quesnoy (MP7, France).

Locus	n	OR	M
P4			
L	1	3.21	–
W	1	2.72	–
M1			
L	1	3.13	–
W	1	4.48	–
M2			
L	1	1.76	–
W	1	3.31	–
p4			
L	1	3.09	–
W	1	1.29	–
m2			
L	2	2.87–3.15	3.01
W	3	1.58–1.94	1.8

Table 2

Measurements (in mm) of the specimens of *Miacis latouri* Quinet, 1966 from Le Quesnoy (MP7, France).

Tableau 2

Mesures (en mm) des spécimens de *Miacis latouri* Quinet, 1966 trouvés au Quesnoy (MP7, France).

Locus	n	OR	M
P4			
L	1	4.06	–
W	0	–	–
M2			
L	1	2.24	–
W	1	4.19	–
p4			
L	3	3.5–3.65	3.55
W	3	1.48–1.58	1.54
m2			
L	1	3.46	–
W	2	1.97–2.26	2.16

“MIACIDAE” Cope, 1883

Gracilocyon Smith and Smith, 2010

Emended 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; narrow talonid on p4; high crowned p4 and m1–2; three lower

Table 3

Measurements (in mm) of the specimens of *Vassacyon taxidiotis* sp. nov. from Le Quesnoy (MP7, France).

Tableau 3

Mesures (en mm) des spécimens de *Vassacyon taxidiotis* sp. nov. trouvés au Quesnoy (MP7, France).

Locus	n	OR	M
M1			
L	2	5.54–5.72	5,63
W	2	7.86–8.09	7,97
p1			
L	2	2.07–2.24 ^a	2,16
W	2	1.59–1.69 ^a	1,64
p2			
L	1	2.82	–
W	1	1.46	–
p3			
L	1	4.1	–
W	1	1.95	–
p4			
L	1	4.98	–
W	1	2.24	–
m1			
L	2	6.12–6.72 ^a	6,42
W	2	2.46–2,97 ^a	2,715
m2			
L	1	4.38	–
W	1	2.25	–
m3			
L	2	1.87–2.82 ^a	2,35
W	1	1.95 ^a	–
MD	2	8.92–11.69	10.35
H			

Weight = 1.34 kg^b

^a Estimated on the basis of the roots.

^b Weight estimated after Van Valkenburgh (1990).

molars with long talonid basin; P4 with large parastyle, short postmetacrista and large protocone; M1 with triangular outline, nearly symmetrical styler shelf with long and labially oriented postmetacrista, deep ectoflexus, and antero-posteriorly short protocone; M2 short and wide with well-developed styler shelf (after Smith and Smith, 2010).

Type species: *Gracilocyon winkleri* (Gingerich, 1983).

Other species: *Gracilocyon rosei* (Heinrich et al., 2008); *Gracilocyon igniculus* (Beard and Dawson, 2009) comb. nov.; *Gracilocyon solei* Smith and Smith, 2010; *Gracilocyon rundlei* (Hooker, 2010) comb. nov.

Type locality: North America, Big Horn Basin, Wasatchian (Wa0–Wa2).

Distribution: North America, Red Hot local fauna, Wasatchian (Wa-M?), Big Horn Basin, Wasatchian (Wa0–Wa2); Europe, MP7, Dormaal (Belgium), Le Quesnoy (France); MP8 + 9, Abbey Wood (England).

Gracilocyon solei Smith and Smith, 2010

(Fig. 1)

Diagnosis: “*Gracilocyon solei* 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 (Smith and Smith, 2010).

Type locality: MP7, Dormaal (Belgium)

Distribution: MP7, Dormaal (Belgium), Le Quesnoy (France)

Holotype: M1, IRSNB M1327 (DIII314RS) (L)

Referred specimens from Le Quesnoy: P4, MNHN QNY2-2520 (R); M1, MNHN QNY2-2517 (L), MNHN QNY2-2546 (R); M2, MNHN QNY2-2510 (R); p4, MNHN QNY2-2618 (R); m2, MNHN QNY2-2522 (R), MNHN QNY2-2528 (L); m3, MNHN QNY2-2533 (L)

Measurements: Table 1.

Description: the morphology of the P4 is unusual. The parastyle, which is clearly separated from the paracone by a notch, is well developed. The paracone is high and tilted distally. The protocone is large and close to the paracone. The tooth is peculiar in having a very short postmetacrista. Moreover, the postmetacrista is weakly shifted distally. There is no lingual cingulum on P4. The P4 is weakly secant and thus appears primitive among “miacids”.

The M1 is highly triangular in occlusal view. The paracone and metacone are connate until mid-height. The paracone is the highest cusp. The preparacrista is long, and slightly shifted mesially. The postmetacrista is clearly individualized by a notch. It is only shorter than the preparacrista, and is slightly shifted distally. The styler shelf is developed. There is a deep ectoflexus. The protocone is shorter than the labial part. The profossa is narrow. The paraconule and metaconule are present. The metaconule is the smallest one. There is a small postparaconule crista. There are pre- and postcingula, and they are not fused.

Like the M1, the M2 is triangular and elongated transversely. The paracone and metacone are connate. The preparacrista is long and transversely oriented. The metastyle is worn. The styler shelf is developed, and a small ectoflexus is present. The protocone is shorter than

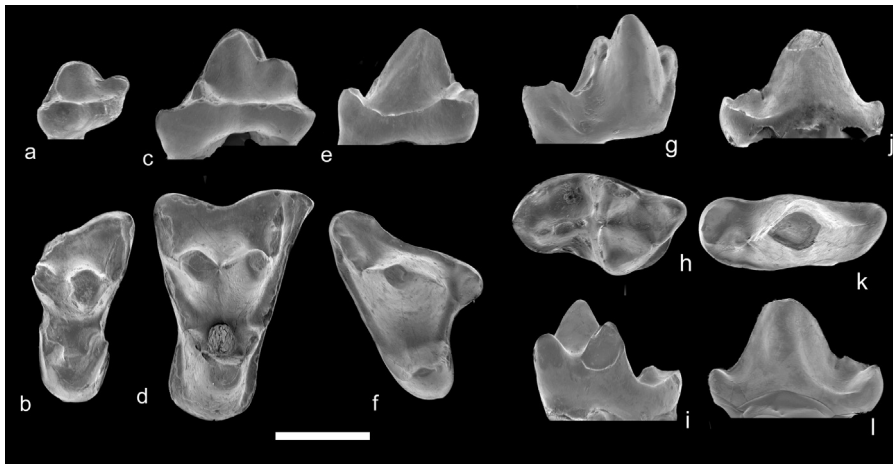


Fig. 1. *Gracilocyon solei* Smith and Smith, 2010 from Le Quesnoy (MP7, France): a–b: MNHN QNY2-2510, M2: a: labial view; b: occlusal view; c–d: MNHN QNY2-2546, M1: c: labial view; d: occlusal view; e–f: MNHN QNY2-2520, P4: e: labial view; f: occlusal view; g–i: MNHN QNY2-2522, m2: g: labial view; h: occlusal view; i: lingual view; j–l: MNHN QNY2-2618, p4: j: labial view; k: occlusal view; l: lingual view. SEM Photographs. Scale bar: 2 mm.

Fig. 1. *Gracilocyon solei* Smith and Smith, 2010 du Quesnoy (MP7, France): a–b: MNHN QNY2-2510, M2: a: vue labiale; b: vue occlusale; c–d: MNHN QNY2-2546, M1: c: vue labiale; d: vue occlusale; e–f: MNHN QNY2-2520, P4: e: vue labiale; f: vue occlusale; g–i: MNHN QNY2-2522, m2: g: vue labiale; h: vue occlusale; i: vue linguale; j–l: MNHN QNY2-2618, p4: j: vue labiale; k: vue occlusale; l: vue linguale. Photographies au MEB. Barre d'échelle: 2 mm.

the labial part. The paraconule is large and related to the parastyle as on M1. The metaconule is lower and smaller than the paraconule. A small postparaconule crista is present. Only a precingulid is present.

The p4 is high, pointed, and elongated mesiodistally. It is nearly symmetrical in lateral view. The paraconid is individualized, projected mesially and high. The talonid is slightly narrower than the protoconid. The hypoconulid is well separated from the hypoconid. The hypoconid is labially located. The hypoconulid is more centrally located; it is also distally shifted. The hypoconid is high. There are pre- and postcingulids, which are not fused. The entoconid crest is reduced.

The m2 is small. The trigonid is pointed, especially the protoconid. The metaconid and paraconid are well separated. Only their bases are in contact. The metaconid is slightly higher than the paraconid. The metaconid is slightly distal to the protoconid. The talonid is elongated mesiodistally. It is oblique (distally shifted labially). The postfossid is narrow. The hypoconid is high and the cristid obliqua is well oblique (distally shifted labially). The entocristid, which is also oblique, is low. The hypoconid and hypoconulid are separated. The entoconid is not present. The pre- and ectocingulids are well defined.

The m3 is only known by a trigonid fragment. The trigonid is small, but is pointed. The protoconid is only slightly higher than the metaconid and paraconid.

Discussion: Smith and Smith (2010) erected the genus *Gracilocyon* for a small “miacid” from the Belgian locality of Dormaal, *Gracilocyon solei*. They also referred to this new genus two small “miacids” from the Early Wasatchian of North America: *Gracilocyon rosei* (Wa0) and *Gracilocyon winkleri* (Wa0–Wa1). *Gracilocyon* clearly differs from the contemporaneous “miacids” *Miacis*, *Uintacyon* and *Vassacyon* by the presence of numerous primitive features.

Gracilocyon is notably characterized by a primitive M1: the tooth is triangular in occlusal view with a developed styler shelf, close paracone and metacone, postmetacrista almost as long as the preparacrista, and a preparacrista shifted mesially, small cingula, and presence of a developed metaconule and a postparaconule crista. The P4 is also characteristic of the genus because it displays a possible derived feature: well-individualized and high paraconid. Finally, the lower molars are plesiomorphic in displaying long and narrow talonids, and high and pointed trigonids.

The fossils discovered in Le Quesnoy are morphologically similar to the reference material from Dormaal described by Smith and Smith (2010). They present all the distinctive features of the genus *Gracilocyon*. Moreover, their sizes are close to those of the specimens of *G. solei* from Dormaal. The m2 from Le Quesnoy are only slightly larger than those of Dormaal. However, these differences do not justify a specific distinction.

Interestingly, the specimens from Le Quesnoy present a new tooth position for *G. solei*: the P4. The tooth is characterized, like the M1, by a primitive morphology: the postmetacrista is shorter and the protocone and parastyle are more developed than in other “miacids”.

Hooker (2010) recently described a new “miacid” species – *Miacis rundlei* – based on several isolated teeth found in Abbey Wood (MP8 + 9, England). Among them, he noted the presence of an unusual P4 characterized by a very short postmetacrista. The morphology of the P4 found in Le Quesnoy clearly resembles the P4 found in Abbey Wood.

Hooker (2010) also remarked that *M. rundlei* displays numerous primitive dental features among “miacids” and noted that the closest taxon to *M. rundlei* “appears to be *Miacis rosei*” from the Wa-0. The primitive features of *M. rundlei*, such as the acute trigonid on molars and

triangular outline of the M1 clearly remind of *Gracilocyon solei* from Dormaal (MP7) and Le Quesnoy. Interestingly, *M. rosei*, which is considered to be close to *M. rundlei* has been referred to *Gracilocyon* (Smith and Smith, 2010).

Based on the morphologies of the premolars and molars, we thus propose a new generic attribution for the species: *Gracilocyon rundlei* (Hooker, 2010) comb. nov.

The specimens of *Gracilocyon solei* from Le Quesnoy, like those from Dormaal, differ from *Gracilocyon rundlei* by a more transversely elongated M1, larger styler shelf on M1, less developed paraconid on p4, and less mesiodistally compressed trigonid on the molars. These features are primitive among “miacids”. However, it is worth noting that the p4s from Le Quesnoy and Abbey Wood share a wider talonid (derived feature) than on the specimens from Dormaal.

Beard and Dawson (2009) recently described *Miacis igniculus* based on a fragmentary p4. It represents the smallest species of the genus. The p4 is similar to the specimens of *Gracilocyon solei* and *G. winkleri* in having a very narrow talonid compared to the earliest *Miacis* species. The peculiar morphology of *M. igniculus* thus resembles more a *Gracilocyon* species (e.g. *G. winkleri*) than *Miacis*. We therefore propose to refer the Mississippian taxon as *Gracilocyon igniculus* (Beard and Dawson, 2009) comb. nov.

Conclusion: *Gracilocyon solei* is now recorded in Le Quesnoy. As indicated by Smith and Smith (2010), this species is a morphological ancestor to the North American species *G. rosei* and *G. winkleri*.

A new dental locus, the P4 is represented in the material from Le Quesnoy. As for the upper molars, the P4 shows a very primitive morphology. Moreover, the peculiar morphology of the tooth (presence of a large parastyle, a short postmetacrista and a large protocone) supports a close relationship with the European species *Gracilocyon rundlei* from Abbey Wood (MP8 + 9). This relationship implies an endemic evolution of the genus in Europe. Smith and Smith (2010) showed that *G. solei* was more primitive than *Gracilocyon winkleri*, and proposed a dispersal from Europe to North America for this genus.

The genus *Gracilocyon* appears to be very plesiomorphic among “Miacidae”. The upper teeth notably have a morphology that recalls those of the “insectivorous” cimolestids. One of the few derived features of *Gracilocyon* is possibly the enlargement of the paraconid on the premolars. The genus *Gracilocyon* thus appears very conservative among the “Miacidae”.

As noted by Smith and Smith (2010), *Oodectes* (Wasatchian and Bridgerian of North America) represents the closest genus from *Gracilocyon*. The P4 found in Le Quesnoy appears morphologically similar to that of *Oodectes*; this is important because the P4 is characteristic of the latter genus, as noted by Heinrich (1997). The material from Le Quesnoy clearly supports the close relationship between the two genera. Finally, despite the primitive features of *Gracilocyon* and *Oodectes*, the two genera have their own evolution, notably characterized by an increase of the size of the premolars, which are almost of the same size in *Oodectes* (Heinrich, 1997).

***Miacis* Cope, 1872**

Diagnosis: “Carnassial and tubercular dentition well differentiated, carnassials and premolars moderate to large, tubercular dentition small, lower molars with basined heels, M1 in early forms with small hypocone, slender or moderately deep jaw with the symphyseal region comparatively shallow and loosely sutured, and typically a full eutherian dentition, with M3 vestigial or absent in some species (after Matthew, 1909, p. 345, 362). *Miacis* is the most generalized of the early miacids, and it is, in practice, identified chiefly by the absence of characteristics distinguishing the other contemporary genera” (Gingerich, 1983).

Type species: *Miacis parvivorus* Cope, 1872.

Included species: *Miacis sylvestris* Marsh, 1872; *Miacis washakius* Wortman, 1901; *Miacis hargerii* Wortman, 1901; *Miacis medius* Matthew, 1909b; *Miacis latidens* Matthew, 1915; *Miacis exiguus* Matthew, 1915; *Miacis hookwayi* Stock, 1934; *Miacis gracilis* Clark, 1939; *Miacis latouri* Quinet, 1966; *Miacis deutschii* Gingerich, 1983; *Miacis petilus* Gingerich, 1983; *Miacis australis* Gustafson, 1986; *Miacis cognitus* Gustafson, 1986.

Miacis latouri Quinet, 1966

(Fig. 2)

Type locality: Dormaal (Belgium), MP7, Early Eocene

Distribution: Europe, MP7, Dormaal, Erquelinnes (Belgium), Le Quesnoy (France)

Emended diagnosis: *Miacis latouri* shares with the North American genera *Miacis* and *Vulpavus* derived features such as the presence of a wide talonid on p4 and molars, reduced entoconid on molars, developed cingula on molars. *Miacis latouri* differs from the oldest North American *Miacis* species by a smaller size, a more gracile morphology, and primitive features such as a narrower talonid and postfoscid, a more pointed trigonid on m2, a less mesiodistally compressed trigonid on m2, M1 with more triangular outline, M1 with more symmetrical styler shelf, a more developed metastylar area on the upper molars, and less developed pre- and postcingula on M1.

Holotype: M1, IRSNB M1360 (R)

Paratype: m2, IRSNB M75 (R)

Type locality: MP7, Dormaal (Belgium)

Distribution: MP7, Dormaal (Belgium), Le Quesnoy (France)

Referred specimens from Le Quesnoy: P4, MNHN QNY2-2619 (L); M2, MNHN QNY2-2534 (R); p4, MNHN QNY2-2553 (R), MNHN QNY2-2554 (L), MNHN QNY2-2523 (L); m2, MNHN QNY2-2624 (L), MNHN QNY2-2511 (L)

Measurements: Table 2.

Description: the protocone of the isolated P4 found in Le Quesnoy (MNHN QNY2-2619) is broken, but it was certainly mesially shifted. The P4 is clearly the upper carnassial tooth: the postmetacrista is elongated and well projected distally. A distinct but poorly developed parastyle is visible. A continuous labial cingulum is present.

One M2 (MNHN QNY2-2534) is known from Le Quesnoy. The teeth are slightly triangular in occlusal view. The paracone and metacone are low and elongated mesiodistally. The paracone is higher than the metacone, but the difference in height is feeble. The postmetacrista is absent. The styler shelf is present but reduced. The protofossa is

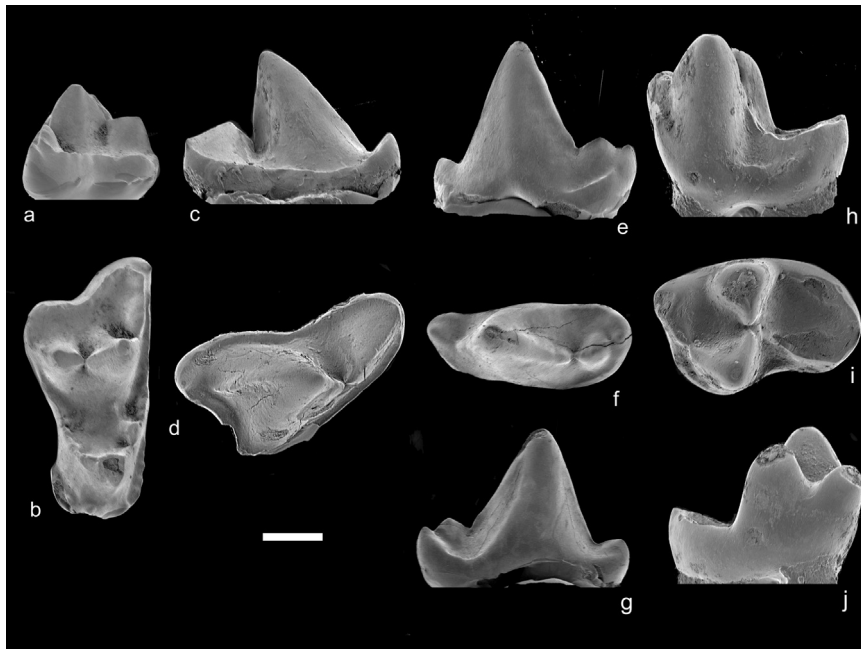


Fig. 2. *Miacis latouri* Quinet, 1966 from Le Quesnoy (MP7, France): a–b: MNHN QNY2-2534, M2: a: labial view; b: occlusal view; c–d: MNHN QNY2-2619, P4: c: labial view; d: occlusal view; e–g: MNHN QNY2-2553 p4: e: labial view; f: occlusal view; g: lingual view; h–j: MNHN QNY2-2624, m2: h: labial view; i: occlusal view; j: lingual view. SEM photographs. Scale bar: 1 mm.

Fig. 2. *Miacis latouri* Quinet, 1966 du Quesnoy (MP7, France): a–b: MNHN QNY2-2534, M2 a: vue labiale; b: vue occlusale; c–d: MNHN QNY2-2619, P4: c: vue labiale; d: vue occlusale; e–g: MNHN QNY2-2553 p4: e: vue labiale; f: vue occlusale; g: vue linguale; h–j: MNHN QNY2-2624, m2: h: vue labiale; i: vue occlusale; j: vue linguale. Photographies au MEB. Barre d'échelle: 1 mm.

much narrower than the styler shelf, but is long. The paraconule is well individualized. The metaconule is reduced compared to the metaconule of the M2 in *Gracilocyon solei*. The protocone is as high as the metacone. The pre- and postcingula are present; they are not fused lingually.

Three p4s have been found at Le Quesnoy: MNHN QNY2-2553, MNHN QNY2-2554 and MNHN QNY2-2523. The paraconid is well individualized, but it is lower than in *Gracilocyon*. The protoconid is low, elongated mesiodistally and robust. The talonid is short, but as wide as the protoconid. There are two cusps on the talonid: the hypoconid is the highest and is labially located. The hypoconulid is distally located, and is more centrally located than the hypoconid. There is a developed entocristid. There are pre- and postcingulids in the labial part of the p4.

Two m2s have been found in Le Quesnoy. The trigonid is wide, poorly elevated and slightly mesiodistally compressed. The paraconid and metaconid have almost the same height. The protoconid is not much more elevated than the paraconid and metaconid. The metaconid is more distally located than the protoconid. The paraconid is poorly projected mesially. The talonid is only slightly narrower than the trigonid. The talonid is shorter than the trigonid. The postfossid is wide. The hypoconid is the highest cusp, and the entocristid becomes lower toward the lingual part. The entoconid and hypoconulid are poorly individualized and no notch is present.

Discussion: the European *Miacis latouri* was previously only known based on two upper molars: M1 and M2 (Quinet, 1966).

The P4, p4, M2, and m2 found in Le Quesnoy are clearly more robust and larger (15–25%) than those of *Gracilocyon solei*. The M2s have more developed cingula and more separated paracone and metacone than in *Gracilocyon* species. The morphologies of these teeth clearly recall the M2 found in Dormaal (IRSNB M 75) and referred to *Miacis latouri* by Quinet (1966).

The p4s of *Miacis latouri* have a less developed paraconid, but possess a wider talonid and a developed entocristid compared to the p4 of *G. solei*. This morphology resembles that of *Miacis exiguus*. The P4 displays a longer postmetacrista and less developed parastyle than the P4 of *Gracilocyon solei*. The m2s have a notably lower trigonid and wider talonid than the m2s known for *Gracilocyon solei*.

The seven specimens discussed in this part clearly differ from those of *Gracilocyon*. Their distinctive features closely resemble the oldest North American *Miacis* species such as *Miacis exiguus* and *Miacis deutschii*.

At present, only three *Miacis* species are recorded in North America during the Early Wasatchian (Wa-M?/Wa-4): *Miacis igniculus* (Wa-M?), *Miacis deutschii* (Wa-2), and *Miacis exiguus* (Wa-3/Wa-4). As discussed above, *M. igniculus* is referred to the genus *Gracilocyon*.

The oldest *Miacis* species thus is *Miacis deutschii* from Wa2-Wa3 (Heinrich et al., 2008). However two isolated teeth from Wa0 have been referred to *Miacis*: one m1 has been referred to *Miacis deutschii* (Strait, 2001) and one m2

has been referred to cf. *Miacis deutschii* (Rose et al., 2012). Only the m2 can be compared with the material from Europe at present. The North American specimen is larger (3.65 mm. vs. 3.46 mm.) and differs by a more reduced entoconid (derived feature).

The specimens of *Miacis latouri* differs from North American *Miacis* species, notably *Miacis deutschii*, by a more developed parastyle on P4, a more pointed trigonid and narrower and longer talonid on m2, less mesiodistally compressed trigonid on m2, M1 with more triangular outline, M1 with more symmetrical styler shelf, more developed metastylar area on upper molars, less developed pre- and postcingula on M1. The fossils of *Miacis latouri* also appear more gracile than those from North America.

Beard and Dawson (2009) recently referred to *Miacis* sp. one m2 and one M3 from the Red Hot local fauna (Wa-M?). Only the m2 can be compared at present with the material from Dormaal and Le Quesnoy. The m2 from the North American locality differs by its smaller size, but also by a shorter talonid (derived features).

Conclusion: *Miacis latouri* was the only Early Eocene “miacid” species known in Europe for a long time. Teilhard de Chardin (1922) first recognized the presence of Carnivora at the Dormaal locality. *M. latouri* was described by Quinet (1966) based on two specimens found in this locality. Since this work, numerous specimens have been found in Dormaal, but they have not been formally described yet. However, these discoveries permitted the description of a second species in Dormaal: *Gracilocyon solei* (Smith and Smith, 2010).

Based on the material from Le Quesnoy, three new tooth positions are known: P4, p4, and m2. The fossils support a close relationship with the *Miacis* species from North America. The study of the “miacid” fossils shows that the European form represents a taxon slightly more primitive than the *Miacis* species known in North America, but the oldest North American *Miacis* species are poorly known. It is possible that *Miacis* dispersed from Europe to North America during the Palaeocene-Eocene boundary, as proposed for *Gracilocyon* by Smith and Smith (2010) and *Vassacyon* (see below).

***Vassacyon* Matthew, 1909**

Diagnosis: “Premolars reduced and spaced, increasing in size posteriorly; upper molars with short parastyle, small to well-developed hypocone; m1 with large, broadly basined talonid, m2 with low trenchant talonid” (Heinrich et al., 2008).

Type species: *Vassacyon promicrodon* (Wortman and Matthew, 1899).

Included species: *Vassacyon boweni* Heinrich, Strait and Houde, 2008; *Vassacyon taxidiotis* sp. nov.

Occurrence: North America, Wasatchian, Wa0-Wa5 (Clarks Fork and Bighorn basins); Europe, MP7 (Le Quesnoy, France).

Vassacyon taxidiotis sp. nov.

(Figs. 3 and 4)

Diagnosis: *Vassacyon taxidiotis* is smaller than the North American *Vassacyon promicrodon* (7%–25% depending on the locus). *Vassacyon taxidiotis* differs from *V. promicrodon*



Fig. 3. *Vassacyon taxidiotis* sp. nov. from Le Quesnoy (MP7, France): a–c: MNHN QNY2-2547, left lower jaw bearing m2, alveoli of canine, p1, m1 and m3 and roots of p2, p3, anterior root of p4: a: lingual view; b: labial view; c: occlusal view. Scale bar: 1 cm. d–e: MNHN QNY2-2505, M1: d: occlusal view; e: labial view; d–e: SEM photographs. Scale bar: 1 mm.

Fig. 3. *Vassacyon taxidiotis* sp. nov. du Quesnoy (MP7, France): a–c: MNHN QNY2-2547, mâchoire inférieure gauche portant la m2, les alvéoles des p1, m1 et m3 et les racines des p2 et p3, et la racine antérieure de la p4: a: vue linguale; b: vue labiale; c: vue occlusale. Barre d'échelle: 1 cm. d–e: MNHN QNY2-2505, M1: d: vue occlusale; e: vue labiale. d–e: Photographies au MEB. Barre d'échelle: 1 mm.

by primitive features: more asymmetric p4, more pointed trigonid on m2, narrower talonid on m2, higher paracone, more developed styler shelf, more developed metastylar area, longer preparacrista, more developed “hook” on M1, and less developed hypocone. *Vassacyon taxidiotis* is probably smaller than the North American *V. boweni*.

Etymology: From Greek *taxidiotis*, traveller.

Type locality: MP7, Le Quesnoy (France).

Holotype: MNHN QNY2-2548, right dentary fragment with p2, p3 and p4, alveoli of p1, m1, m2 and m3

Referred specimens: MNHN QNY2-2547, left dentary fragment with m2, alveolus of canine, p1, p2, p3, p4, m1 and m3; M1, MNHN QNY2-2505 (R), MNHN QNY2-2532 (R), MNHN QNY2-2535 (R); p3, MNHN QNY1-397 (R), MNHN QNY2-2502 (R); m2, MNHN QNY2-2507 (L)

Measurements: Table 3.

Description: Two complete M1 and one labial fragment are known for the new species. The paracone and metacone are low and almost fully separated. The metacone is much smaller than the paracone. The preparacrista is short and transverse. There is an important mesial extension (“hook”) on the parastyle. The postmetacrista is very reduced and low. The metastylar area is short. The protocone area is only slightly shorter than the labial area. The paraconule is large, while the metaconule is present but reduced compared to the paraconule. The pre- and postcingula are well

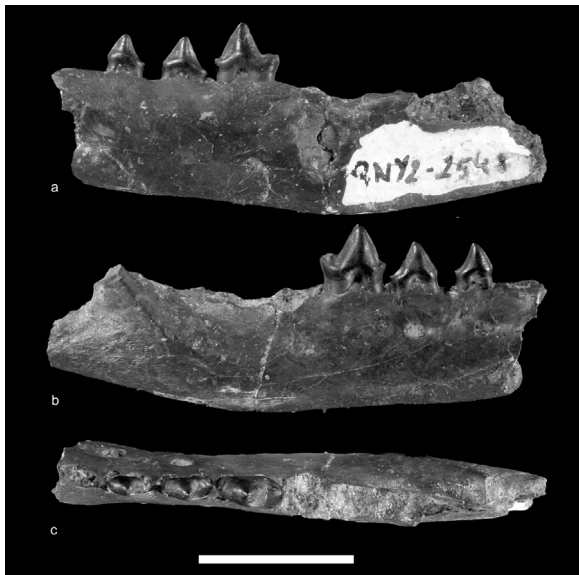


Fig. 4. *Vassacyon taxidiotis* sp. nov. from Le Quesnoy (MP7, France): a–c: MNHN QNY2-2548 (Holotype), right lower jaw bearing p2, p3 and p4, alveoli of p1, m1, m2 and m3: a: lingual view; b: labial view; c: occlusal view. Scale bar: 1 cm.

Fig. 4. *Vassacyon taxidiotis* sp. nov. du Quesnoy (MP7, France): a–c: MNHN QNY2-2548 (Holotype), mâchoire inférieure droite portant les p2, p3 et p4, les alvéoles des p1, m1, m2 et m3: a: vue linguale; b: vue labiale; c: vue occlusale. Barre d'échelle: 1 cm.

developed. However, they are not fused lingually. There is a small hypocone. The styler shelf is short and the ectoflexus is almost absent.

Two dentaries are known: MNHN QNY2-2547 and MNHN QNY2-2548. On the two specimens, the mental foramina are present below p1–p2, and below p3. The p2 is separated from p1 and p3 by small diastemata. MNHN QNY2-2548 differs from MNHN QNY2-2547 by a narrower depth under the m1, a constant depth along the dentary and smaller diastemata. The first feature is considered to be related to sexual dimorphism in *Uintacyon rudis* by Gingerich (1983). MNHN QNY2-2547 and MNHN QNY2-2548 thus could represent respectively male and female individuals.

The p1 is only known by its alveolus. The tooth is single-rooted in the two dentaries. The p2 is present on MNHN QNY2-2548. The tooth is two-rooted and asymmetric in lateral views. There is no paraconid. The talonid is very short and narrow. A single tiny cusp (hypoconid?) is present. The p3 is higher, wider and longer than the p2. The p3 is slightly more symmetric than the p2. However, there is no paraconid. As on p2, the talonid is short and narrow. It is located very low. One single (hypoconid?) cusp is present. The p4 is distinctly larger than the p3. The tooth appears also more robust. The paraconid is small and low. The protoconid is high, and its apex appears located mesially because of the asymmetry of the tooth. The talonid is higher than the paraconid. The talonid is wide but is slightly narrower than the protoconid. The hypoconid is located slightly labially, while the hypoconulid is more centred transversely on the talonid. The talonid cusps are very close and poorly separated. The entocristid is high. There are pre- and postcingulids. They are clearly visible, but they are not fused.

Unfortunately, no m1 is known. The alveoli present on MNHN QNY2-2547 and MNHN QNY2-2548 show that the m1 is much larger than the m2 and m3. However, its morphology is unknown. The m2 is present on MNHN QNY2-2547, but is worn, and MNHN QNY2-2518 corresponds only to a labial part. The paraconid is slightly projected mesially. The trigonid is not compressed mesiodistally. It is slightly pointed. The talonid is slightly narrower than the trigonid. The talonid is elongated mesiodistally and slightly oblique (distally shifted labially). The m3 is small and single-rooted on the two dentaries. As for the m1, its morphology is unknown.

Discussion: The genus *Vassacyon* was previously only known in North America. Two species from the Wasatchian (Early Eocene) have been referred to the genus: *V. bowni* (Wa0) and *V. promicrodon* (Wa2–5) (Gingerich, 1983; Heinrich et al., 2008). *Vassacyon bowni* is currently known only by two M2s. They differ from those of *V. promicrodon* by a smaller size, less developed hypocone, and more developed metaconule. These features being primitive, *V. bowni* is considered as the most primitive *Vassacyon* species in North America (Heinrich et al., 2008). Beard and Dawson (2009) recently described two lingual fragments of M1 from the Red Hot local fauna (Wa-M?) that they referred as cf. *Vassacyon*.

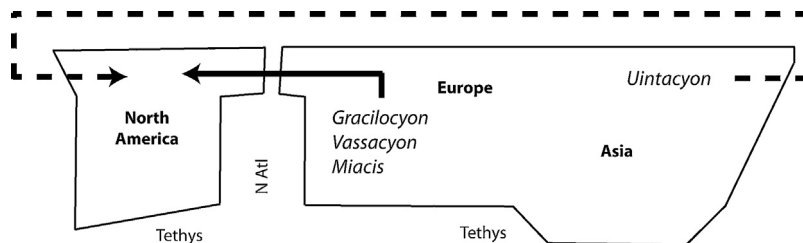


Fig. 5. Faunal dispersals illustrated by the “Miacidae” near the P/E boundary. Abbreviations: N Atl: North Atlantic. Dashed line: Late Paleocene dispersal (Clarkforkian); solid line: possible Paleocene/Eocene boundary dispersal. Adapted after Gheerbrant and Rage (2006) (Fig. 1).

Fig. 5. Échanges fauniques lors de la transition Paléocène–Éocène soutenus par les « Miacidae ». Abréviations: N Atl: Atlantique nord. Ligne pointillée: dispersion au Paléocène supérieur (Clarkforkien); ligne pleine: dispersion envisagée pendant la limite Paléocène/Éocène. Adapté de Gheerbrant et Rage (2006) (Fig. 1).

Vassacyon taxidiotis shares with the North American *V. promicrodon* the presence of diastemata between the p2 and p3, a hypoconulid higher than the hypoconid on p4, and a poorly mesially projected paraconid, the developed cingulids, the presence of a metaconule on M1. These features are primitive among the “Miacidae”. They also share the presence of a wide talonid with high entocristid on p4, low and separated paracone and metacone, small styler shelf and a small hypocone on molars. These derived features are distinctive of *Vassacyon* among the Early Eocene “miacids”. *Vassacyon taxidiotis* thus appears more derived than *Miacis latouri* and *Gracilocyon solei*. *Vassacyon taxidiotis* and *V. promicrodon* also share a deep mandible compared to *Gracilocyon* and the oldest *Miacis* species.

Vassacyon taxidiotis differs from *V. promicrodon* by a more asymmetric p4, more pointed trigonid on m2, narrower talonid on m2, higher paracone, more developed styler shelf, more developed metastyler area, longer preparacrista, presence of a developed “hook”, shorter protocone, less developed hypocone, and unfused pre- and postcingula. All these features are primitive among the “Miacidae”. *Vassacyon taxidiotis* appears more primitive than *V. promicrodon*, but this is not surprising because *V. promicrodon* is unknown before the Wa2 (Gingerich, 1983), while the fauna of Le Quesnoy is considered equivalent to that of the Wa0 (Nel et al., 1999; Solé et al., 2011). Finally, *Vassacyon taxidiotis* is smaller than *V. promicrodon*: the teeth of the latter are between 7% and 25% larger than those of the European species.

As indicated above, the oldest and most primitive North American species of *Vassacyon* – *V. bowni* (Wa0) – is only known by M2. Unfortunately, no M2 is known for the new European species. *V. bowni* thus cannot be directly compared to the European *Vassacyon*. However, we can notice that *Vassacyon taxidiotis* and *V. bowni* are primitive among *Vassacyon* in having separated pre- and postcingula and more developed styler shelf than in *V. promicrodon*. We established expected sizes of the M2 of *V. taxidiotis* based on the sizes of *V. promicrodon*. The expected length for the M2 of *V. taxidiotis* is 3.37 mm and the expected width is 3.7 mm. These dimensions are smaller than those of *V. bowni* (L = 3.8–4.0 mm.; W = 5.8–6.5 mm.). However, the width of the expected M2 of *V. taxidiotis* is underestimated because, as shown by Heinrich et al. (2008), *V. promicrodon* is characterized by a transverse reduction of the M2.

The M1 from Le Quesnoy differ from the two fragments described by Beard and Dawson (2009) from Wa-M? by smaller and less bunodont paraconule and metaconule and narrower postcingulum. The morphology of the French specimens is clearly more primitive.

Conclusion: *Vassacyon taxidiotis* sp. nov. from Le Quesnoy (MP7) clearly agrees with the morphology known for the North American genus *Vassacyon*. *Vassacyon taxidiotis* is distinctly smaller and more primitive than *V. promicrodon* (Wa2–Wa5). It is notably more primitive in the morphology of the p4 and M1. It is currently impossible to compare *V. taxidiotis* and *V. bowni* because they are not known by similar loci. However, the expected dimensions of the M2 of *Vassacyon taxidiotis* are smaller than those of *V. bowni* (see above), but the small size of *V. taxidiotis* compared to *V. bowni* remains presently uncertain.

The presence of a *Vassacyon* species in Europe is important because it shows that the “Miacidae” were as diversified in this continent as in North America.

Based on the small size of *Vassacyon taxidiotis* and its primitive features, a European origin for the North American *Vassacyon* can be hypothesized. This implies a dispersal from Europe to North America around the Palaeocene–Eocene boundary. Moreover, the two other taxa present in Le Quesnoy – *Miacis latouri* and *Gracilocyon solei* – also indicate dispersal from Europe to North America (see above). However, it is worth keeping in mind that the primitive status of *V. taxidiotis* compared to *V. bowni* is not well supported at present.

4. General discussion

Biostratigraphic implications

The P/E boundary is located between the MP6 and MP7 reference-levels. It is marked by the first appearance of the “modern” mammals such as perissodactyls, primates, and artiodactyls in Europe, as in North America. The carnivorous mammals are involved in the faunal interchange of the P/E boundary: “miacids”, hyaenodontids and oxyaenids appeared in Europe just after the P/E boundary (Godinot, 1982; Hooker, 1998; Smith and Smith, 2001; Smith et al., 2010; Solé et al., 2011).

The Belgian locality of Dormaal, which is the reference-locality of level MP7, represents the earliest European locality from the Early Eocene (Smith et al., 2006). Two “miacid” species have been described from this locality: *Gracilocyon solei* and *Miacis latouri*. Several specimens found in Le Quesnoy clearly belong to these two taxa. Their sizes and morphologies agree with those observed on the Dormaal specimens. These similarities indicate that Le Quesnoy lies close to the MP7 level as proposed by Nel et al. (1999) based on the entire faunas, and Solé et al. (2011) based on Oxyaenidae. Moreover, because the “miacid” specimens do not show differences with those of Dormaal, this suggests that Le Quesnoy and Dormaal are very close in age.

Diversity of the “Miacidae” in Europe in the Earliest Eocene

The European “Miacidae” were previously known by two species and genera only recorded in the Belgian basin: *Miacis latouri* and *Gracilocyon solei* (Quinet, 1966; Smith and Smith, 2010). The study of the “miacids” from Le Quesnoy increases the generic diversity of the “Miacidae” during the beginning of the Early Eocene with the identification of *Vassacyon taxidiotis*. The recent descriptions of *Gracilocyon* and *Vassacyon* show that the European “Miacidae” were almost as diversified as they were in North America at the same period. Only the genus *Uintacyon*, which is recorded since the Late Palaeocene in North America is missing in MP7 localities.

The diversity of the European “miacids” was equal to that of the hyaenodontidae present in the Early Eocene localities, both groups being represented by three species. The “miacids” are slightly more numerous than the oxyaenidae, the latter being known by two taxa (Smith and Smith, 2001; Solé et al., 2011). *Gracilocyon* represents a very small carnivorous species close in size to

the hyaenodontid *Prototomus minimus* Smith and Smith, 2001. *Miacis latouri* is intermediate between *Gracilocyon solei* and *Vassacyon taxidiotis* and is almost equal in size to the hyaenodontid *Arfia gingerichi* Smith and Smith, 2001. *Vassacyon* is characterized by a crushing and grinding dentition, whereas *Gracilocyon* possesses a puncturing dentition. These differences in dental morphology underline an adaptive diversity in “miacids” similar to that recorded in hyaenodontids (Smith and Smith, 2001) and large oxyaenids (Smith and Smith, 2001; Solé et al., 2011). Thus, the taxonomic diversity and the morphologic diversity of the “miacidae” were equivalent to that of the hyaenodontids in Europe. The diversity of the “miacids” indicates that this group represented an important component of the European ecosystems during the earliest part of the Early Eocene.

Finally, the new reference of the English *Gracilocyon rundlei* implies that the genus *Gracilocyon* had at least a short endemic evolution in Europe.

Implications of the European “miacids” concerning the dispersal events around the P/E boundary

The monophyly of the Carnivoramorpha (Viverravidae + “Miacidae” + Carnivora) is well supported (Wesley-Hunt and Flynn, 2005), but its geographic origin remains enigmatic. The oldest and most complete specimens of Carnivoramorpha are referred to Viverravidae. The latter are mostly known in North America – but also in Asia (Meng et al., 1998) – where they are highly diversified since the Torrejonian (Middle Palaeocene) (Gingerich and Winkler, 1985; Meehan and Wilson, 2002; Polly, 1997). Fox and Youzwyshyn (1994) and Fox et al. (2010) described very primitive carnivoramorphans fossils from Puercan localities (Early Palaeocene). However, these fossils are not referred to Viverravidae or “Miacidae”. The present available data thus support a North American origin for the Viverravidae (and probably the Carnivoramorpha), but the geographic origin of the “Miacidae” remains uncertain. As indicated above, the oldest occurrence of a “miacid” is *Uintacyon rudis* from the latest part of the Palaeocene of North America (Clarkforkian) (Fig. 5). However, this taxon is probably an immigrant because it shows numerous derived features (Gingerich, 1983). Smith and Smith (2010) proposed that *Uintacyon* dispersed from Asia to North America via the Bering Bridge during the Late Palaeocene.

The morphological diversity of the Early Eocene European “miacids” supports an important Palaeocene radiation of the “miacids” that is currently not recorded in the fossil record (see also Heinrich et al., 2008). Despite the undetermined geographic origin of the “miacidae”, the fossils found in Europe in both Dormaal and Le Quesnoy show that Europe was a central area for the dispersal of the “miacidae” in Laurasia around the Palaeocene-Eocene boundary. The absence of *Uintacyon* from the earliest part of the Early Eocene in Europe shows that this genus followed a dispersal route different from that of *Vassacyon*, *Gracilocyon* and *Miacis*. The dispersal of *Uintacyon* probably followed the Bering land Bridge, as proposed by Smith and Smith (2010) (Fig. 5). Numerous other mammalian groups support the existence of faunal dispersals between Asia and North America near the P/E boundary (Beard, 1998) (Fig. 5). As indicated above, Smith and Smith (2010) showed that

Gracilocyon solei was more primitive than *Gracilocyon winkleri*, and proposed a dispersal from Europe to North America for this genus. Our present study of *Vassacyon taxidiotis* shows that the latter species is possibly smaller and more primitive than the North American ones. This suggests a possible dispersal of *Vassacyon* from Europe to North America (Fig. 5). It is probable that the genus *Miacis* followed a similar dispersal way (Fig. 5).

Because the genera *Miacis*, *Gracilocyon* and *Vassacyon* are known in the Wa0 (Gingerich, 1989; Heinrich et al., 2008; Rose et al., 2012), the “miacids” known in Dormaal and Le Quesnoy probably dispersed to North America just after the P/E boundary. This pattern agrees with the dispersals recorded for other mammal groups at this time (Godinot and Lapparent de Broin, 2003; Smith and Smith, 2001; Smith et al., 1996, 2006). Eberle and McKenna (2002) and Eberle and Greenwood (2012) noticed the presence of *Miacis* sp. and cf. *Vulpavus* in Ellesmere Island (Nunavut). This supports a dispersal through the De Geer route.

Hooker (1996, 1998) criticized the relevance of the Mammalian Palaeogene Reference levels for the Early Eocene (MP7–MP10). He used previously published faunal lists to propose a more formal succession of five intervals, defined as “concurrent range biozones” (Zones PE I to V), valid for Northwest Europe only. These five zones have been defined in order to better understand the mammalian faunal interchanges of the Palaeocene/Eocene boundary in Northwest Europe. Because Dormaal is referred to PEI zone, Le Quesnoy should also be referred to this zone. The first occurrence of *Miacis*, *Gracilocyon* and *Vassacyon* can now be used for defining both MP7 level and PEI zone.

Interestingly, Rich (1971) and Hooker (2010) referred several specimens respectively from Abbey Wood (MP8 + 9, PEIII zone) and Avenay (MP8 + 9, PEV zone) as cf. *Uintacyon*. Their mention of this genus in localities younger than Dormaal and Le Quesnoy could imply a second dispersal of “miacid” during the Early Eocene, but with a different direction. *Uintacyon* probably dispersed from North America to Europe during the earliest part of the Early Eocene. Indeed, because the age of Abbey Wood is possibly 55.12 Ma (Hooker, 2010), *Uintacyon* could have dispersed only 400 ky after the Palaeocene-Eocene boundary. Finally, the first occurrence of *Uintacyon* could allow defining the PEIII, PEIV and PEV zones and the MP8 + 9 level.

5. Conclusion

The study of the “miacid” fossils from the French locality of Le Quesnoy allows us to identify a new species of *Vassacyon*, a genus previously unknown in Europe. Its small size and primitive morphology lead us to propose a European origin for the species known in North America. Moreover, its discovery increases the diversity of the “miacidae” in Europe: three morphologically distinct genera are now recorded in the earliest Eocene.

The other fossils found in Le Quesnoy have been referred to the previously known *Miacis latouri* and *Gracilocyon solei*. Their discovery supports an age close to that of Dormaal (reference-locality of the MP7 level) for Le Quesnoy.

More importantly, the discovery of a P4 of *Gracilocyon* supports the reference of the recently described *Miacis rundlei* from Abbey Wood (MP8+9) to the genus *Gracilocyon*, and also supports close relationships with the North American genus *Oodectes*.

However, the MP7 “miacid” fauna remains poorly related to Early and Middle Eocene “miacid” faunas because the MP8+9 and MP10 “miacids” are presently poorly known.

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