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Dispersals of placental carnivorous mammals (Carnivoramorpha, Oxyaenodonta & Hyaenodontida) near the Paleocene-Eocene boundary: a climatic and almost worldwide story

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ABSTRACT. During the Late Paleocene and around the Paleocene-Eocene boundary, there were important mammalian dispersals in Laurasia involving earliest modern mammals such as rodents, primates, perissodactyls, and artiodactyls. The placental carnivorous mammals (Viverravidae, "Miacidae", Hyaenodontida, Oxyaenodonta) importantly took part in these dispersals. The present article shows that these latter mammals allow reconstructing faunal dispersal scenarios during the early Paleogene. Indeed, they evidenced several dispersal ways among Laurasia, but also with Africa and possibly India. The dispersal phases discussed in the present paper concern the Early Paleocene, Late Paleocene, latest Paleocene (Clarkforkian NALMA), and Paleocene-Eocene transition.

KEYWORDS: Paleobiogeography, "Miacidae", Viverravidae, Hyaenodontidae, Oxyaenidae.

1. Introduction

The sea level was high during the major part of the Paleocene. Asia and Europe were separated by the Obik Sea, which joined the Artic and the Tethys seas (Iakovleva et al., 2000, 2001), while North Africa was separated from Laurasia by a major seaway, the Tethys (Gheerbrant & Rage, 2006). North America probably had few connections with Asia and Europe, and only few mammals dispersed (Missiaen, 2011). Europe consisted of several isolated islands. The Western Interior Seaway, which divided North America in two parts, disappeared during the Paleocene. These marine barriers clearly limited mammalian faunal interchanges inside Laurasia, and favoured endemic evolution during the major part of Paleocene. However, several small-scale dispersals occurred during the Paleocene between North America and Asia (Beard, 2002; Smith et al., 2004; Smith et al., 2010; Missiaen, 2011; Smith, 2013), Africa and Europe (Gheerbrant & Rage, 2006; De Bast et al., 2012), and possibly between Europe and Asia or North America (Smith & Smith, 2001; Hooker. & Dashzeveg, 2003; Smith et al., 2006).

The latest part of the Paleocene, the Clarkforkian (56.8-55.8 Ma) North American Land Mammal Age (NALMA), corresponds to a short period of global warming between the cooler Early and Middle Paleocene and the very warm Early Eocene (Fig. 1). This global warming favoured dispersals among Laurasia, at least from Asia to North America (Rose, 1981; Beard, 2002).

The conjunction of a major lowering of the sea level and of a global warming near the P/E boundary favoured large-scale faunal exchanges: the Mammal Dispersal Event (MDE; Fig. 1) (e.g., Smith et al., 2006). This global Paleocene-Eocene Thermal Maximum (PETM) – or Initial Eocene Thermal Maximum (IETM) – corresponds to an important increase of the temperatures (from 8 to 12°C in the ocean) during a short interval of time (< 170 000 years) (Zachos et al., 2001, 2003, 2008) (Fig. 1). This global warming allowed the extension of the tropical rainforest to latitude 50°, of the paratropical rainforest to 60-65°, of broad-leaved evergreen forest to 70°, and of deciduous broad-leaved trees and deciduous conifers farther north (Manchester, 1999; Eberle & Greenwood, 2012). The reptiles and mammals recorded in the Ellesmere Islands supports this floristic extension to the North Pole (Eberle & McKenna, 2002; Eberle & Greenwood, 2012). The temperature probably importantly decreased after the PETM (Wing et al., 2000), but a second important warming, the Early Eocene Climatic Optimum (EECO), which corresponds to a much longer period (53-50 Ma) of high temperature, occurred during Early and Middle Eocene (Fig. 1). However, it appears not to be related to important mammal dispersals conversely to the PETM; indeed, only few immigrants are recorded in North America (Woodburn et al., 2009).

The following holarctic Mammal Dispersal Events (MDEs) have been proposed:

(1) Between Asia and North America through Bering land bridges (Beard, 1998). Even if no fossil has been found in high latitude for the Bering land bridges road, the presence of similar taxa in Asia and North America during Early Eocene supports the occurrence of faunal interchanges between the two continents.
(2) Between Europe and North America through the De Geer and Thulean route (Smith & Smith, 2001; Smith et al., 2006). The excavations performed in the Ellesmere Islands, which were located on the passageway of the De Geer route, yielded a vertebrate fauna composed of crocodilians and mammals (Eberle & McKenna, 2002; Eberle & Greenwood, 2012). This fauna clearly supports a faunal interchange between Europe and North America through the De Geer route.
(3) Between Europe and Asia through the Turgai strait (Godinot & Lapparent de Broin, 2003; Hooker & Dashzeveg, 2003). Moreover, Iakovleva et al. (2000; 2001) showed that major sea falls of the Siberian Sea allows the emersion of the Turgaï strait, which probably favoured mammal dispersals.

Dispersal events have also been proposed between Europe and Africa (Gheerbrant & Rage, 2006). The faunal interchanges probably occurred through the Mediterranean Tethyan Sill (Apulian or Alboran plates).

In this paper, we analysed the dispersals of the specialized placental carnivorous mammals (Carnivoramorpha, Oxyaenodonta and Hyaenodontida) because they are interesting for the paleobiogeographic reconstructions of the Paleocene – especially the Late Paleocene – and Paleocene-Eocene transition because they were importantly involved in the faunal exchanges that occurred at these times and support several dispersal ways.

2. The fossil record of placental carnivorous mammals

2.1. The placental carnivorous mammals (Carnivoramorpha, Oxyaenodonta and Hyaenodontida)

The Carnivoramorpha, Oxyaenodonta and Hyaenodontida, which are presently grouped in the Ferae, are placental mammals that are carnivorously adapted (Flynn & Wesley-Hunt, 2005). Because of their diet, they possess very particular dental, cranial and postcranial features. The most striking dental feature of the carnivorous mammals is the presence of specialized shearing teeth – the carnassial teeth. This latter feature allows distinguishing the Carnivoramorpha, Oxyaenodonta and Hyaenodontida from the Mesonychia (Acreodi). The Mesonychia represent the largest placental carnivorous mammals from the Paleocene and Eocene (Morlo et al., 2010). However, because they do not belong to the Ferae, they will not be discussed in the present study.

The Carnivoramorpha, Oxyaenodonta and Hyaenodontida are distinguished based on the position of the carnassial teeth and the number of molars (Flynn & Wesley-Hunt, 2005; Rose, 2006). The carnassial teeth of the Carnivoramorpha are located in P^4 and

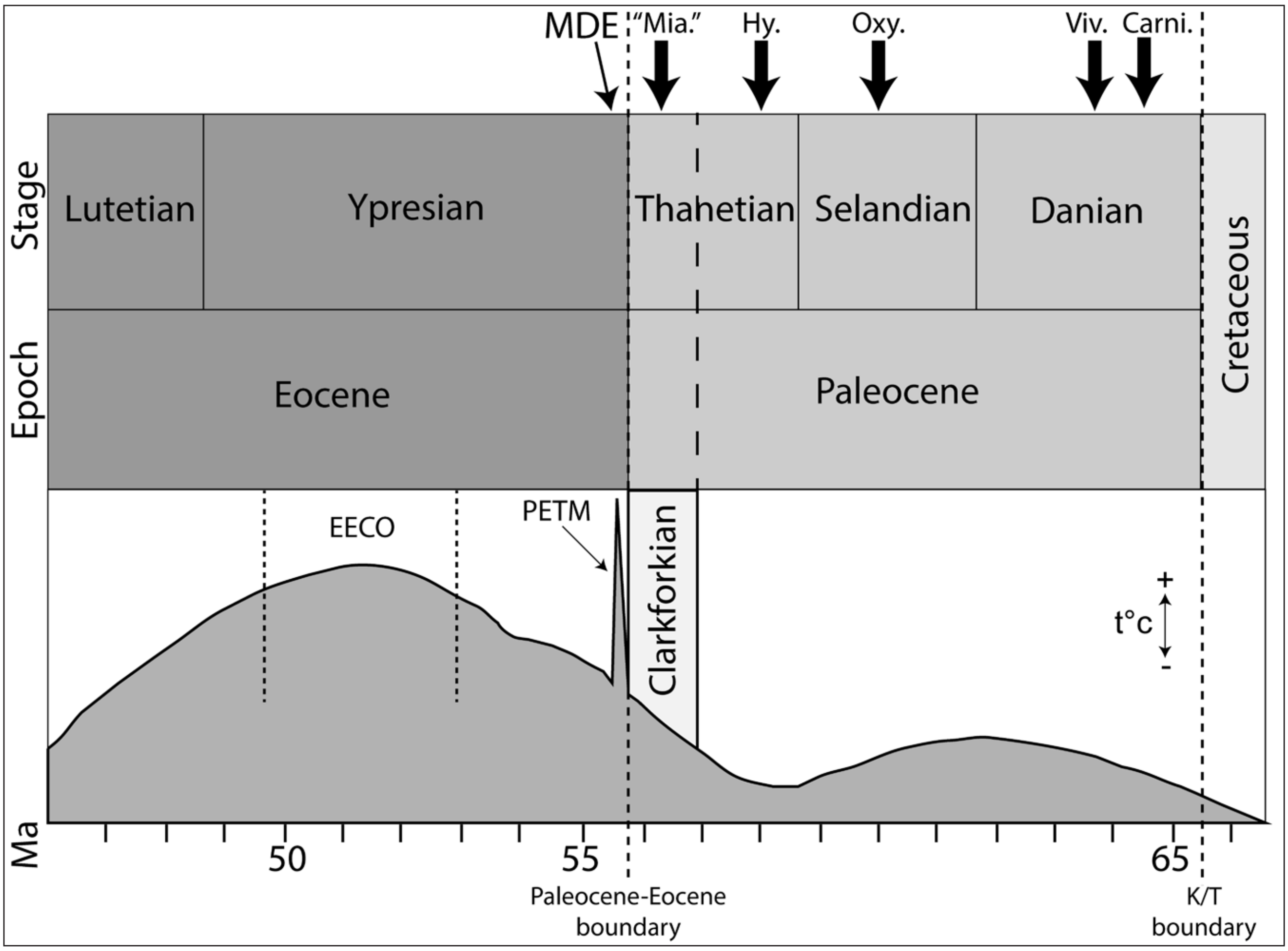

Figure 1. Stratigraphic scale with indications of the first record for each group of placental carnivorous mammals. "Mia." = Miacidae, Hy. = Hyaenodontida, Oxy. = Oxyaenodonta, Viv. = Viverravidae, Carni. = Carnivoramorpha, MDE = Mammal Dispersal Event, EECO = Early Eocene Climatic Optimum, PETM = Paleocene-Eocene Thermal Maximum. The temperatures are from Zachos et al. (2001, 2008).

M_1, while they are located more posteriorly in the Oxyaenodonta and Hyaenodontida. Moreover, these latter groups generally possess more numerous molars than the carnivoramorphans. These carnivorous mammals also share several basicranial and tarsal similarities. They notably possibly share the presence of an ossified tentorium (bony shelflike projection separating parts of the brain). However, it is not clear whether these similarities are synapomorphic or whether they are more likely primitive (Flynn & Wesley-Hunt, 2005). Moreover, the presence of carnassial teeth is a possible convergent adaptation toward similar diet (Fox & Youzwyshyn, 1994; Muizon & Lange-Badré, 1997).

For a long time, Oxyaenodonta and Hyaenodontida were considered as primitive carnivorous mammals related to the ancestry of the Carnivoramorpha, and were groups together in "Creodonta". In this view, the evolution of the carnivorous mammals was characterized by a continuous trend toward more anterior carnassial teeth. However, the "Creodonta" group has been criticized and is considered to be diphyletic (Polly et al., 1994, 1996; Morlo et al. 2009; Solé, 2013). Solé (2013) proposed to use Oxyaenodonta and Hyaenodontida.

2.2. Carnivoramorpha

The Carnivoramorpha include the Viverravidae, the Miacidae and the crown group Carnivora (= Caniformia + Feliformia). The oldest carnivoramorphans are the Viverravidae and the Miacidae; the two groups were importantly diversified in the Paleocene and Eocene (Flynn, 1998). Wesley-Hunt & Flynn (2005) recently proposed, based on phylogenetic analysis that the Viverravidae are monophyletic and the sister group of the Miacidae+Carnivora, while the "Miacidae" are a paraphyletic group, which is basal to Carnivora (see also Flynn et al., 2010).

Fox and Youzwyshyn (1994) and Fox et al. (2010) described very primitive carnivoramorphan fossils from Puercan localities (Early Paleocene) of North America (Fig. 1). However, these fossils are referred neither to Viverravidae nor to "Miacidae".

2.4.1. Viverravidae

The Viverravidae are characterized by the absence of M^3 and M_3 (Flynn, 1998; Flynn et al., 2010). Except the fossils from the Puercan, the oldest specimens of Carnivormorpha are referred to Viverravidae (Fig. 1) (Fox and Youzwyshyn, 1994; Meehan & Wilson, 2002). The latter are mostly known in North America, where they are diversified since the Torrejonian (Middle Paleocene) to Late Eocene (Gingerich and Winkler, 1985; Polly, 1997; Flynn, 1998; Meehan and Wilson, 2002). The Viverravidae are also well-known in Asia (Fig. 2), where they ranged from Early Paleocene (Shanguan ALMA) to Late Eocene (Qiu & Li, 1977; Wang, 1978; Huang & Zheng, 2005; Tong & Wang, 2006).

However, the dentition of the Asian viverravids differs from that of the North American ones as noted by Gingerich & Winkler (1985). One of the most striking differences is the very reduced M^2 and M_2 of the Asian taxa. It is worth mentioning that the Sarcodontidae (*e.g.*, *Hyracolestes*, *Carnilestes*), which are known in Asia from Early Paleocene to Middle Eocene, are distinguished from the other "insectivorous" mammals from Asia by dentition more carnivorously adapted, and by the absence of M^3 and M_3. For instance, the sarcodontines, such as *Carnilestes*, are characterized by a carnassial-like P^4 (Wang & Zhai, 1995; Lopatin & Kondrashov, 2004); indeed, its morphology is similar to that of the carnivoramorphans. These observations question the referral of the Asian genera such as *Pappictidops* and *Orientictis* to the Viverravidae.

If we consider that the Asian taxa do belong to the Viverravidae, then North America and Asia could both pretend to be the centre of origin of Viverravidae. However, the Viverravidae importantly radiated in North America, conversely to Asia, where

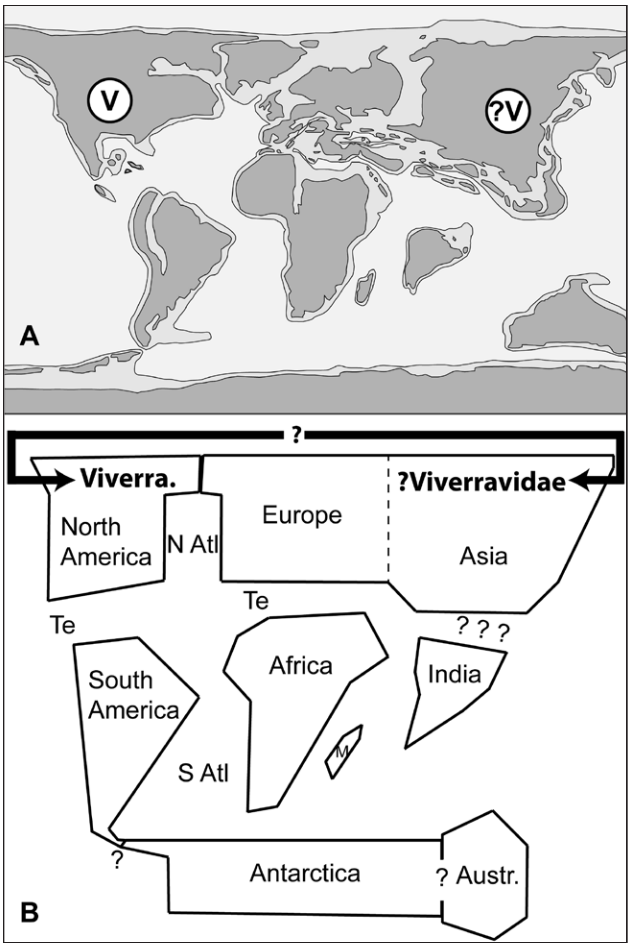

Figure 2. A. Geographic distribution of the placental carnivorous mammals during the Early Paleocene. White circle = possible centre of origin of the carnivorous group. The presence of the Viverravidae in Asia is questionable (see text). B. Faunal dispersal during the Early Paleocene. Because the centre of origin is unknown for the Viverravidae, the way of dispersal between North America and Asia is uncertain (see text). Abbreviations: V = Viverravidae; Viverra. = Viverravidae; N Atl = North Atlantic; S Atl = South Atlantic; Te = Tethys; ? = uncertain connections; M. = Madagascar. [A: adapted from Ron Blakey, Tertiary-Cretaceous, http://www2.nau.edu/rcb7/065Marect.jpg; B: adapted from Gheerbrant & Rage (2006, fig. 1)].

the diversity is more restricted (Gingerich & Winkler, 1985). North America thus seems the most probable centre of origin of the Viverravidae.

2.4.2. *"Miacidae"*

The "Miacidae", which primitively possess the M^3 and M$_3$, are poorly known in the Paleocene. The oldest occurrence of a "miacid" is *Uintacyon rudis* from the latest Paleocene of North America (Clarkforkian) (Fig. 1). However, this taxon is probably a migrant because it displays numerous derived features. Moreover, it is too derived to be at the root of "Miacidae" (Gingerich & Deutsch, 1989). More recently, Smith et al. (2010) evidenced the presence of a "miacid" in a new Late Paleocene European locality (Rivecourt). The preliminary study of this fossil shows that it does not belong to *Uintacyon*, but it is also too derived to be at the root of the "miacids" (Solé, 2010). The geographic origin of the "Miacidae" thus remains uncertain because of the very poor Paleocene record of this group. However, Solé (2010), based on his review of the oldest "miacids" give arguments for an Asian origin of the "miacids" (e.g., absence of "miacids" from Europe and North America until latest Paleocene; appearance of the "miacids" in North America and Europe at the same time that the rodents; presence of taxa close to *Uintacyon* in the Early Eocene of Asia). Finally, the existence of two distinct "miacid" taxa in the Late Paleocene importantly supports a Paleocene radiation of the "miacids" that is not presently evidenced in the fossil record. Heinrich et al. (2008) had the same conclusion based on the analysis of the earliest North American "miacids".

2.3. Hyaenodontida

The Hyaenodontida, most of which possess three molars (the exception being apomorphic limnocyonines), were present in Africa (late Palaeocene to Miocene), Asia (late Palaeocene to Miocene), Europe (Eocene to Miocene), and North America (Eocene to Oligocene). However, the origin of the Hyaenodontida remains uncertain. Beard (1998) and Meng et al. (1998) favoured an Asian origin based on the discovery of the limnocyonine *Prolimnocyon chowi* from the Late Palaeocene (Gashatan) of China. However, several recent arguments better support an African origin (Gheerbrant, 1995; Gheerbrant et al., 2006; Solé et al., 2009; Solé, 2013). Indeed, two distinct hyaenodontidan species have been found in the Late Paleocene of Africa: (1) Gheerbrant (1995) described *Tinerhodon disputatum* from the Ouarzazate Basin (Morocco) and (2) Solé et al. (2009) published *Lahimia selloumi* from the Ouled Abdoun Basin (Morocco). Conversely to *Tinerhodon*, which presents a very primitive dental morphology, *Lahimia* distinguishes by the loss of p1 and secant molars; these latter features allow referring this genus to the Koholiinae. For Gheerbrant et al. (2006), Solé et al. (2009) and Solé (2013) the diversity of the Hyaenodontida in the Paleocene of Africa – and also in entire the Paleogene – supports an African origin. This origination presently dates from the Late Paleocene (Fig. 1).

2.4. Oxyaenodonta

The Oxyaenodonta represent the largest representatives of the Ferae from the Late Paleocene to Middle Eocene. They are characterized, as the Viverravidae, by the absence of M^3 and M$_3$. They also had more specialized shearing dentition than the hyaenodontidans and carnivoramorphans. The Oxyaenodonta surely originated in North America (Middle Paleocene) where they have their oldest fossil record (Fig. 1). Indeed, *Tytthaena*, which is the most primitive oxyaenodontan, has been described by Gingerich (1980) based on specimens from the Middle Paleocene of Wyoming (middle Tiffanian). Moreover, the Oxyaenodonta mainly radiated in North America (Gunnell, 1998). However, they are also known in Early Eocene of Europe (Smith & Smith, 2001; Hooker, 2010; Solé et al., 2011) and in Middle Eocene of Asia (Granger, 1938).

3. The dispersals of placental carnivorous mammals during the early Paleogene

3.1. Early Paleocene dispersal

The presence of Viverravidae in Early Paleocene of North America (MacIntyre, 1966) and Asia (Wang, 1978) suggests the existence of connexion between these two landmasses during the beginning of Paleogene (Fig.2A). This connexion is also supported by the presence of mesonychids and pantodonts in the two continents (Missiaen, 2011). However, the present poor knowledge of the history of the earliest viverravids does not allow further interpretation concerning the dispersal(s) that occurred between North America and Asia during the Early Paleocene (Fig. 2B).

3.2. Late Paleocene dispersal

The hyaenodontidans are known in the Late Paleocene of Africa and Asia (Meng et al., 1998; Gheerbrant, 1995; Solé et al., 2009) (Fig. 3A). A Late Paleocene age of the Gashatan fauna, from which the hyaenodontidan limnocyonine *Prolimnocyon chowi* is known, has been confirmed by stratigraphical and geological studies (Bowen et al., 2005; Meng et al., 2007). The presence of this limnocyonine species in Asia implies a faunal dispersal between Africa and Asia before the P/E boundary (Fig. 3B). However, the dispersal path is unknown.

Several faunal dispersals between Africa and Laurasia have been recorded in the Early Paleogene (Gheerbrant & Rage, 2006). However, the earliest recorded faunal dispersals occurred only between Africa and Euramerica; the direct dispersals between Asia and Africa only occurred at the Middle Eocene favoured by the activation of the Iranian route (Gheerbrant & Rage, 2006).

Because the Limnocyoninae are unknown in Europe and North America until the Early Eocene, dispersal from Africa to

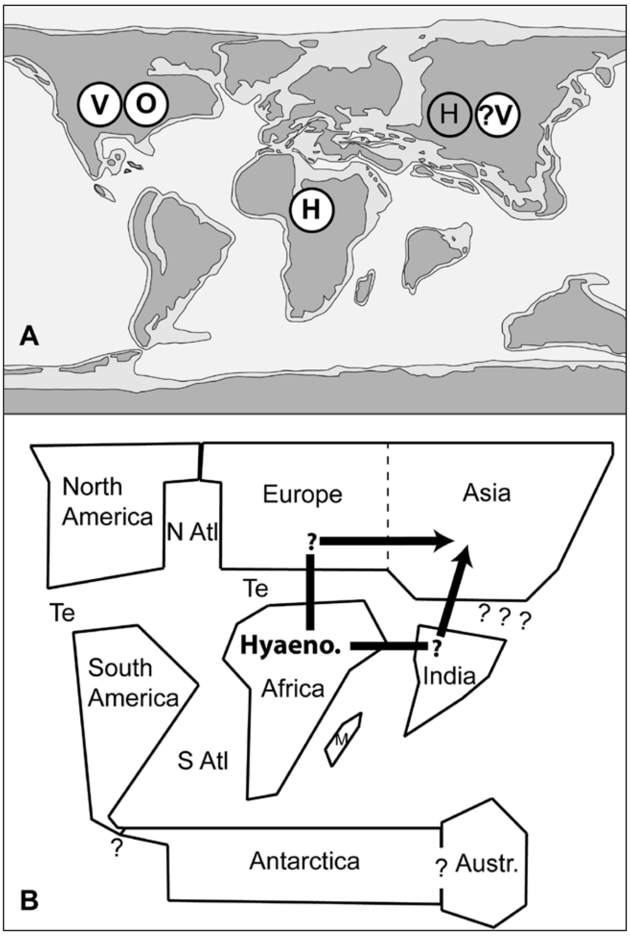

Figure 3. A. Geographic distribution of the placental carnivorous mammals during the Late Paleocene. White circle = possible centre of origin of the carnivorous group. B. Faunal dispersal during the Late Paleocene. Abbreviations: V = Viverravidae; O = Oxyaenodonta; H = Hyaenodontida; Hyaeno. = Hyaenodontida; N Atl = North Atlantic; S Atl = South Atlantic; Te = Tethys; ? = uncertain connections; M. = Madagascar. The dispersal way of the Hyaenodontida from Africa to Asia is presently uncertain. [A: adapted from Ron Blakey, Tertiary-Cretaceous, http://www2.nau.edu/rcb7/065Marect.jpg; B: adapted from Gheerbrant & Rage (2006, fig. 1)].

Asia through Euramerica is not presently supported. We thus can hypothesize that India plays a role for the dispersal of the Limnocyoninae from Africa to Asia (Fig. 3B). However, there is presently little evidence for a mammalian dispersal event between Africa and Asia through India. The only direct evidence of connection between Africa and India could concern the adapisoriculid "insectivores" which may have dispersed from India to Africa at the beginning of the Tertiary (Prasad et al. 2010; Smith et al., 2010; Goswani et al., 2011; De Bast et al., 2012).

Finally, the explanations of the presence of hyaenodontidans in Asia remain hypothetical (dispersal through India *vs* through Euramerica) because they are not congruent with the presently known ways of dispersals and with their respective timing (Fig. 3B).

3.3. Latest Paleocene dispersals

The Clarkforkian NALMA (latest Paleocene) begins with the first occurrences of the rodents, the tillodonts, the pantodont *Coryphodon*, and the condylarth *Haplomylus*. It ends with the first occurrences of the perissodactyls, the artiodactyls, the adapiform and the omomyid primates, and the hyaenodontid creodonts (Rose, 1981; Anemone & Dirks, 2009). For a long time, an European equivalent of the Clarkforkian NALMA was missing in Europe. However, several localities, which have been referred to MP6b, could represent this lateral equivalent. These localities are those from the Spanish Tremp Formation, from the Romanian "Calcaires de Rona", and the recently discovered French locality of Rivecourt (López-Martínez & Peláez-Campomanes, 1999; Gheerbrant et al., 2000; Smith et al., 2010). They are characterized, as in North America, by a mixture of typical Paleocene and Early Eocene taxa (e.g., rodents, "miacids", Lousinidae).

Paleontological studies evidenced dispersals between Asia and North America during the Clarkforkian (Beard, 1998, 2002; Missiaen, 2011). Among the carnivorous mammals only "miacids" are involved in these dispersals. They appeared during the Clarkforkian in North America and MP6b in Europe (Fig. 4A). The Paleocene "miacids" are represented by two distinct genera: *Uintacyon* in North America (Gingerich & Winkler, 1985) and a new taxon morphologically close to *Vassacyon* in Europe (Smith et al., 2010; Solé, 2010). The genus *Uintacyon* is unknown in Europe, while *Vassacyon* appears in North America in earliest Wasatchian (Heinrich et al., 2008).

Based on the hypothesis of an Asian origin of the "Miacidae", we propose two distinct dispersals: (1) *Uintacyon* dispersed from Asia to North America through Bering land bridges, while (2) *Vassacyon* dispersed from Asia to Europe, probably through the Turgai strait (Fig. 4B). The hypothesis of two dispersal ways for the "miacids" has been previously proposed by Smith & Smith (2010), but mostly based on Early Eocene "miacids".

It is worth noticing that the "miacids" appeared in Europe and North America at the same time than the rodents, which are considered to originate in Asia. The two groups thus probably dispersed together thanks to climate warming. The recently discovered "miacid" of Europe importantly supports the existence of dispersal between Europe and Asia during the latest Paleocene.

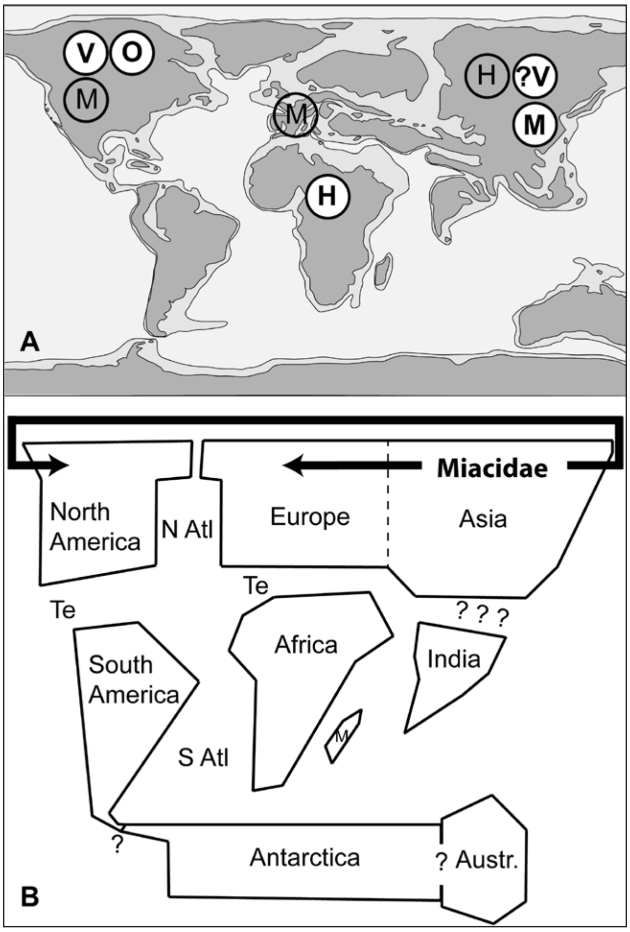

Figure 4. A. Geographic distribution of the placental carnivorous mammals during the latest Paleocene (Clarkforkian, NALMA). B. Faunal dispersal during the Clarkforkian (NALMA, Late Paleocene). Abbreviations: V = Viverravidae; O = Oxyaenodonta; H = Hyaenodontida; M ="Miacidae"; N Atl = North Atlantic; S Atl = South Atlantic; Te = Tethys; ? = uncertain connections; M. = Madagascar. These dispersals are based on the hypothesis of an Asian origin for the "Miacidae"; no "miacid" is presently recorded in Paleocene of Asia. [A: adapted from Ron Blakey, Eocene, http://www2.nau.edu/rcb7/050Marect.jpg; B: adapted from Gheerbrant & Rage (2006, fig. 1)].

3.4. Paleocene/Eocene boundary

The carnivorous faunas appear almost completely homogenized in Laurasia during the earliest Eocene (Fig. 5A) thanks to the dispersals that occurred around the PETM. Indeed, only Asia distinguishes by the absence of Oxyaenodonta.

3.4.1. Viverravidae

The Viverravidae are possibly present in earliest Eocene localities such as Dormaal (Smith, 1999). However, the Viverravidae are clearly present in Abbey Wood (England), which is considered older in age to MP8+9 reference locality (Avenay). Indeed, *Viverravus lawsoni* has been recently described from the English locality (Hooker, 2010). The European species show affinities with the North American representatives (Hooker, 2010) and thus support a dispersal from North America to Europe (Fig. 5B), possibly near the P/E boundary.

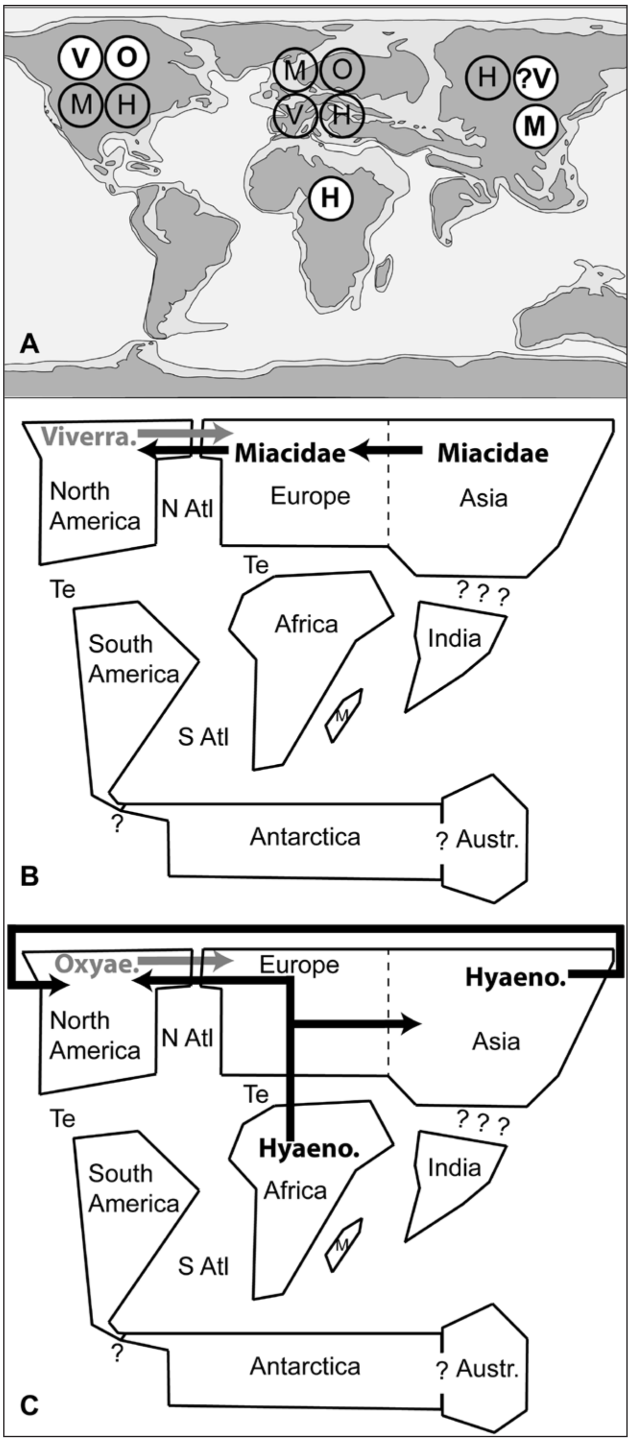

Figure 5. A. Geographic distribution of the placental carnivorous mammals around the Paleocene-Eocene boundary. B & C: Faunal dispersal around the Paleocene-Eocene boundary: B. Viverravidae and "Miacidae", C. Oxyaenodonta and Hyaenodontida. Abbreviations: V = Viverravidae; O = Oxyaenodonta; H = Hyaenodontida; M ="Miacidae"; N Atl = North Atlantic; S Atl = South Atlantic; Te = Tethys; ? = uncertain connections; M. = Madagascar. [A: adapted from Ron Blakey, Eocene, http://www2.nau.edu/rcb7/050Marect.jpg; B & C: adapted from Gheerbrant & Rage (2006, fig. 1)].

3.4.2. "Miacidae"

Two new genera of "miacids" appeared in earliest Eocene in Europe (MP7 level) and North America (Wa0): *Gracilocyon* and *Miacis* (Gingerich, 1989; Heinrich et al., 2008; Smith & Smith, 2010). The study of the two European species, *G. solei* and *M. latouri*, shows that they are ancestral to the North American representatives (Smith & Smith, 2010; Solé et al., 2013). These genera thus support a dispersal from Asia to Europe through the Turgai strait, followed by a dispersal from Europe to North America through the De Geer route (Fig. 5B). *Vassacyon*, which is possibly known in Late Paleocene of Europe (see above), could have followed the same dispersal way from Europe to North America and at the same time because it is recorded from Wa0 (Heinrich et al., 2008).

3.4.3. Hyaenodontida

The Hyaenodontida are represented by numerous genera in Europe. At least 3 genera – *Prototomus*, *Galecyon* and *Arfia* – are known in northern Europe in MP7 level (e.g., Dormaal) (Smith & Smith, 2001). They belong to Arfianinae and Sinopaninae subfamilies (Solé, 2013). In southern Europe, two genera are known: *Parvagula* and *Proviverra* (Godinot, 1981; Godinot et al., 1987). These latter genera are included among Proviverrinae (Solé, 2013). It is worth mentioning that the hyaenodontidans support a North/South division of Europe as proposed by Marandat (1997).

The presence of these three hyaenodontidan subfamilies suggests a dispersal from Africa to Europe through the Mediterranean Tethyan Sill (Fig. 5C) (Solé, 2013).

The Arfianinae and Sinopaninae, which are recorded in earliest Wasachtian (Wa0; Gingerich, 1989), appear more derived than the European ones (Smith & Smith, 2001; Zack, 2011). This supports a dispersal from Europe to North America through the De Geer route (Fig. 5C). Because the Arfianinae are recorded in Early Eocene of Asia (Lavrov & Lopatin, 2004), it is possible that they dispersed from Europe to Asia through the Turgai strait (Fig. 5C).

The Limnocyoninae distinguished from the previously discussed hyaenodontidan subfamilies because they dispersed from Asia to North America through the Bering Land Bridges (Fig. 5C). Indeed, this group, which is known in the Late Paleocene of Asia (Meng et al., 1998), is also known since the earliest Eocene in North America (Wa0; Gingerich, 1989), while they are unknown in Europe for the entire Early Eocene (Smith et al., 2006).

3.4.4. Oxyaenodonta

The European localities of Dormaal, Abbey Wood and Le Quesnoy provided numerous elements of oxyaenodontans such as dental and postcranial material (Smith & Smith, 2001; Hooker, 2010; Solé et al., 2011). Two groups – Palaeonictinae and Oxyaeninae – are recorded in these localities. Each subfamily is represented by one genus, respectively *Palaeonictis* and *Oxyaena*. The Oxyaenodonta surely dispersed from North America to Europe near the P/E boundary because they are only known in North America during the Paleocene (Chester et al., 2010; Hooker, 2010; Solé et al., 2011). They probably dispersed through the De Geer route because they are known in Ellesmere islands (Eberle & McKenna, 2002; Eberle & Greenwood, 2012) (Fig. 5C).

The Oxyaenodonta are reported from the Early Eocene Wutu Formation [China, Bumbanian, *Homogalax* interval following Missiaen (2011)]. However, there are doubts concerning their systematic affinities. Indeed, *Anthracoxyaena* is more similar to hyaenodontidan genus *Arfia* than to Palaeonictinae, and the specimen of *Oxyaena*? sp. shows a three-rooted M^2 as in hyaendontidans, rather than a two-rooted M^2 as in Oxyaenodonta. Besides these taxonomic problems, the timing of the arrival of these Asian taxa is unclear, as their origin (Europe? North America?).

3.5. From the PETM to the EECO

As indicated above, the EECO is a very warm period, which is distinctly longer than the PETM (Fig. 1). However, the dispersals are scarce and poorly known for this period. Conversely to PETM, the EECO seems to have favoured endemic radiation rather than dispersals for the carnivorous mammals. These latter dispersed again in Laurasia but not before the end of the Middle Eocene.

4. Conclusions

Recent finds and phylogenetic reconstructions now permit Paleogene faunal dispersal scenarios to be reconstructed with a fair amount of confidence. They evidenced several dispersal ways among Laurasia, but also with Africa and possibly India. The carnivorous mammals (Carnivoramorpha, Oxyaenodonta, Hyaenodontida) notably support the existence of close relations between Europe and Asia during the Late Paleocene (Clarkforkian) and Early Eocene conversely to what have been thought during years. Moreover, Europe appears central for the dispersal that occurred near the P/E boundary.

Until the PETM event, the dispersals were sporadic, but the MDE interestingly resulted in a homogenisation of the carnivorous faunas in Laurasia. Concerning the Gondwana landmasses, it is important to note that Africa appears apart in having only hyaenodontidan taxa. It is also worth noticing the presence of only hyaenodontidans in Early Eocene of India (Bajpai et al., 2009). This supports a close relationship between Africa and India and supports the origination of Hyaenodontida in Gondwanan area (Solé, 2013).

The two main phases of dispersals (Clarkforkian and PETM) have been triggered by global warming (Fig. 1). However, the EECO surprisingly did not favoured dispersals of the placental carnivorous mammals between continents.-

Finally, the identification of distinct centres of origin for the placental carnivorous mammal groups questions the monophyly of the Ferae. It appears possible that these groups of mammals filled convergently the carnivorous diet niche by developing carnassial teeth. The Ferae thus could be only based on convergences related to carnivorous adaptations than on synapomorphies.

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