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Contributions of Asia to the evolution and paleobiogeography of the earliest modern mammals

by
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KEYWORDS. — paleontology, paleogeography, mammals, Paleocene-Eocene.

SUMMARY. — The mammals, discreet during the dinosaur period, see their size and number of species increase after the extinction of these giants 65 million years ago. This is the beginning of the Age of Mammals. But it is only at the beginning of the Eocene 55 million years ago during an extremely fast and intense global warming called the PETM (*Paleocene Eocene Thermal Maximum*) that their diversity explodes. New groups then suddenly appear on the three northern continents via intercontinental land bridges across which they make important dispersals. These new groups, called “modern mammals”, are the rodents, lagomorphs, perissodactyls, artiodactyls, cetaceans, primates, carnivorans and bats. Although these eight groups represent 83 % of the extant mammal species diversity, their ancestors are still unknown. A short overview of the knowledge and recent progress on this research is here presented based on Belgian studies and expeditions, especially in India and China.

MOTS-CLES. — paléontologie, paléogéographie, mammifères, Paléocène-Eocène.

RESUME. — Les mammifères, discrets durant la période des dinosaures, voient leur taille et leur nombre d’espèces augmenter à partir de l’extinction de ces géants il y a 65 millions d’années. C’est le début de l’Age des mammifères. Mais il faudra attendre l’aube de l’Eocène il y a 55 millions d’années lors d’un réchauffement global extrêmement rapide et intense connu sous le nom de PETM (*Paleocene Eocene Thermal Maximum*) pour voir leur diversité explosée. De nouveaux groupes apparaissent alors soudainement sur les trois continents de l’hémisphère nord grâce à des ponts terrestres intercontinentaux par lesquels ils effectuent de grandes dispersions. Ces nouveaux groupes qualifiés de « mammifères modernes » sont les rongeurs, lagomorphes, périssodactyles, artiodactyles, cétacés, primates, carnivores et chauves-souris. Bien que ces huit groupes représentent 83 % de la diversité des espèces actuelles de mammifères, leurs ancêtres sont encore inconnus. Un bref aperçu des connaissances et progrès récents est présenté ici sur base des études et expéditions belges, en particulier en Inde et en Chine.

TREFWOORDEN. — paleontologie, paleogeografie, zoogdieren, Paleoceen-Eoceen.

SAMENVATTING. — De zoogdieren, die onopvallend waren tijdens de periode van de dinosauriërs, kennen een toename in grootte en aantal na het verdwijnen van deze giganten 65 miljoen jaar geleden. Dit is het begin van de Tijd van de Zoogdieren. Toch is het wachten tot het aanbreken van het Eoceen 55 miljoen jaar geleden tijdens een periode van extreem snelle en intense klimaatopwarming gekend als het PETM (*Paleocene Eocene Thermal Maximum*), tot hun diversiteit werkelijk explodeert. Dan verschijnen plots nieuwe groepen op de drie continenten van de noordelijke hemisfeer dankzij intercontinentale landbruggen waarover ze verre migraties uitvoeren. Deze nieuwe groepen die we de "moderne zoogdieren" noemen zijn de knaagdieren, haasachtigen, onevenhoevigen, evenhoevigen, walvissen, primaten, carnivoren en

vleermuizen. Hoewel deze acht groepen 83% van de huidige soortenrijkdom vertegenwoordigen zijn hun voorouders nog steeds onbekend. Een kort overzicht van de kennis en de recente vooruitgang in dit onderzoek wordt hier gegeven op basis van Belgische studies en veldwerk, in het bijzonder in India en China

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1. Introduction

The earliest known mammals are about as old as the earliest dinosaurs and appear in the fossil record during the late Trias around 220 million years ago with genera such as *Sinoconodon*, *Morganucodon* and *Hadrocodium* (Kielan-Jaworowska *et al.* 2004). However, the earliest placental mammals (Eutheria) are not known before the Early Cretaceous. *Eomaia scansoria* from the Barremian of Liaoning Province, China is the oldest definite placental and is dated from 130 million years ago (Ji *et al.* 2002).

The Mesozoic is clearly the Age of dinosaurs and the mammals that live in their shadow are generally of small size. At the Cretaceous-Tertiary crisis, 65 million years ago, the non-avian dinosaurs get extinct and the mammals diversify to occupy the new ecological niches that are now free. This event marks the start of the Age of mammals. During the Paleocene, that represents the first 10 million years of the Cenozoic, the new mammal orders evolve relatively fast and the first large mammals appear.

At the Paleocene/Eocene boundary, 55.8 million years ago, mammal faunas undergo major evolutionary changes. The majority of modern-type placental orders appear simultaneously in Europe, North America and Asia, while archaic groups persisting since the Paleocene start to decline. These faunistic events, already known since Depéret (1908) have been studied worldwide for the last two decades when it became clear that the Paleocene/Eocene transition represents one of the most critical periods of the Earth Cenozoic history. The mammalian evolution is linked to global migrations during the Paleocene-Eocene transition in the Northern Hemisphere. These gave rise to the first ancestors of the modern mammals such as primates (fig. 1, 2), artiodactyl and perissodactyl ungulates, rodent and lagomorph glires, true carnivores (carnivorans) and other groups on the three northern continents (Smith *et al.* 2006). Modern mammals dispersed to the southern continents only much later allowing marsupials and archaic placentals to survive longer in the southern Hemisphere than in the northern Hemisphere. With the exception of rare bats that are recorded in the Early Eocene of South America (Tejedor *et al.* 2005) and Australia (Hand *et al.* 1994), modern groups do not appear before the Oligocene in the southern Hemisphere.

Our knowledge of the mammal dispersal event on the three northern continents has greatly improved since it has been correlated with a negative Carbon Isotope ($\delta^{13}C$) Excursion - CIE linked to a short greenhouse effect called the Paleocene-Eocene Thermal Maximum - PETM (Magioncalda *et al.* 2004). This PETM is a 150,000 years-lasting abrupt global warming event that represents the warmest period of the last 65 million years. Moreover, several hypotheses and some recent discoveries of Early Eocene mammals suggest that Asia was the center of origin of the modern forms (Beard, 2002; Bowen *et al.* 2002; Hooker & Dashzeveg, 2004; Ni *et al.*, 2004; Smith *et al.*, 2006).

2. Archaic and modern placental mammals

It is commonly admitted that the Cretaceous-Tertiary extinction mainly concerns dinosaurs, large marine reptiles, some invertebrates such as ammonites and belemnites, and a large part of the plankton. Mammals are on the contrary often considered as the winners crossing all the geologic crises. This view is probably far from being real. Mammals indeed survive the Cretaceous-Tertiary crisis but only a few taxa actually cross the Cretaceous-Tertiary boundary. For instance, only one placental genus, *Cimolestes* is known from the latest Maastrichtian and earliest Paleocene and only the orders Leptictida and Cimolesta survive in North America (Archibald 1996). All the other Paleocene orders only appear at or after the Cretaceous-Tertiary boundary. The most well known Paleocene orders are the condylarths, the plesiadapiforms (fig. 3A), the pantodonts, the dinocerates, the mesonychians (fig. 4A) and the oxyaenid creodonts. The Paleocene mammal orders are consider as archaic placental mammals and have also been called Paleoplacentals by opposition to Neoplacentals that are the modern placental mammals (Lucas 2000).

The modern placental mammals are commonly considered as the placental mammal orders that are still present today and that first appear around the Early Eocene. These are mainly primates (fig. 3B), carnivorans, bats, rodents, lagomorphs, perissodactyls, artiodactyls, and cetaceans (fig. 4B) that represent 83 % of the extant species diversity. Other extant groups also appear during the Early Eocene such as proboscidians, hyracoideans, sirenians and macroscelideans. The extant dermopterans and scandentians seem not to be present from the Eocene. These groups are less cosmopolite and are often represented by a low diversity. Their fossil record is also weak and it is thus difficult to determine when they first appeared. Xenarthrans and Pholidotans grouped under the term “Edentates” are still poorly understood and their origin remains one of the mysteries of mammalian evolution (see Rose 2006 for an overview). The hyaenodontid creodonts are a group of carnivorous mammals that appear at the earliest Eocene but disappear during the Miocene. It is thus a modern order but that got extinct before present probably due to competition with carnivorans. The Insectivores represent a wastebasket group of archaic insectivorous orders (formerly grouped under the name Proteutheria) and lipotyphlan insectivores. Among the latter, only the eulipotyphlans constitute the modern insectivores including the erinaceomorphs and soricomorphs.

3. Biodiversity and evolution of mammals from worldwide PETM key localities

Belgium – Europe

The Belgian locality of Dormaal (Flemish Brabant) is the international reference-level for the earliest Eocene mammals of the mammalian biochronological scale for the European Paleogene (level MP7 of Schmidt-Kittler 1987; Smith & Smith 1996). The deposits from the Tienen Formation (called “Upper Landenian” in the former terminology) of this locality are known from 1883 (Rutot & Van Den Broek 1884) and have yielded several basal taxa at the origin of modern groups. Among them, are the oldest European modern mammals such as the primate *Teilhardina belgica* (Teilhard de Chardin 1927; Smith *et al.* 2006; fig. 2), the artiodactyl *Diacodexis gigasei* (Smith *et al.* 1996), hyaenodontid creodonts (Smith & Smith 2001), and carnivorans (Smith & Smith 2010). Next to these important groups are also archaic mammals, crocodilians, trionychid turtles, lizards, boid snakes, amphibians, and lepisosteid and amiid fishes.

The fossil seeds of Dormaal clearly indicate a subtropical environment with an assemblage of fleshy fruits, drupes and berries produced by climbing plants, especially woody lianas (Menispermaceae, Vitaceae and Icacinaceae), aquatic plants (Lythraceae) and trees or shrubs (Nyssaceae) (Fairon-Demaret & Smith 2002). This very warm climate in Belgium 55 million years ago has been confirmed by the identification of the negative Carbon isotope ($\delta^{13}C$) excursion of the PETM based on the analysis of the dispersed organic carbon of the Dormaal sediments (Grimes *et al.* 2006).

Wyoming – North America

The Wilwood Formation of the Bighorn Basin along the Rocky Mountains in Wyoming is famous from the end of the 19 century for its richness in mammal remains from the Early Eocene (Wasatchian) and especially for the earliest Eocene mammals of North America (Gingerich 1989). It is astonishing how closely related are the modern mammal species to those from the Belgian locality of Dormaal. Moreover, the Belgian species belong to the same lineages than the North American ones but are in most cases more primitive (Smith *et al.* 2002; 2006). However, many archaic mammal species are different from those of Belgium suggesting an endemism of the archaic mammals and a cosmopolitism of the modern ones. The Paleocene/Eocene boundary and the PETM have also been identified in several sections containing these earliest modern mammals (Magioncalda *et al.* 2004; Yans *et al.* 2006; Smith *et al.* 2006).

India – South Asia

The oldest fossil mammals from India are restricted to few isolated teeth and postcranial elements of adapisoriculid mammals from the latest Cretaceous of the Deccan Traps indicating Euro-African affinities (Smith *et al.* 2010). The oldest Cenozoic Indian fauna was from the middle Eocene of Kalakot in the Kashmir Himalaya (Ranga Rao 1971; Kumar & Sahni 1985) and shows Asian affinities. The first Early Eocene mammal fauna from India was discovered only recently in the Cambay Formation of Vastan lignite mine in Gujarat, Western India (Rose *et al.* 2006). The fauna includes the earliest modern mammals from the Indian subcontinent, with a high diversity of bats (Smith *et al.* 2007), the first Asian ailuravine rodents (Rana *et al.* 2008), the oldest lagomorphs (Rose *et al.* 2008), primitive adapoid and omomyid primates (Rose *et al.* 2009b), and the first Indian tillodonts (Rose *et al.* 2009a) and basal artiodactyls (Kumar *et al.* 2010). Amazingly, most modern mammals of the Vastan fauna are closely related to European faunas and not to Asian faunas. Isotope analysis indicates that the Vastan deposits do not correspond to the time of the PETM but correspond to the second warm event of the Eocene about 54 million years ago (Clementz *et al.* 2011). The PETM has been identified in deposits of northeastern India but those have not yet yielded vertebrates.

China – Eastern Asia

The Early Eocene locality of Wutu in Shandong Province, East China was for long considered as a key locality to explain the origin and evolution of modern mammals. Although Beard & Dawson (1999) even proposed a late Paleocene age for the Wutu

Formation based on the presence of some primitive mammals with North American affinities such as the neoplagiaulacid multituberculate *Mesodmops dawsonae* and the carpolestid plesiadapiform *Carpocristes oriens*, it is now widely accepted to be of Early Eocene age. This is based on the microevolution of seed-eating carpolestid mammals (Bloch *et al.* 2001). Moreover, the neoplagiaulacid *Mesodmops* and a primitive carpolestid have been discovered in the late Paleocene Chinese fauna of Subeng attesting that these two groups are already present in Asia before the P/E boundary and survive the P/E boundary (Smith *et al.* 2004; Van Itterbeeck *et al.* 2007; Missian & Smith 2008). They are thus relict families in Wutu. Finally, the Early Eocene age is confirmed by a diversified mammal association (51 species) mainly including derived taxa belonging to modern orders such as a hyaenodontid creodont, a miacid carnivoran, several perissodactyls, and an artiodactyl (Tong & Wang 2006). The paleoenvironment and paleoclimate of Wutu is not well understood and is at the moment under the scope of a Sino-Belgian cooperation study project. Next to fossil seeds of *Nuphar* (Nymphaeaceae) recently described (Chen *et al.* 2004) from Wutu are fossil seeds from the oldest definite *Prunus* (Prunoideae) (Li *et al.* 2011). Carbon isotope analysis is also under progress but the PETM has not been identified.

However, the PETM has been recorded in the Lingcha Formation, Hunan Province, South China in the locality where the primate *Teilhardina asiatica* has been discovered (Bowen *et al.* 2002; Ni *et al.* 2004). This species has thus the same age or is slightly older than *Teilhardina belgica* from Belgium but it is also the closest related species among the five *Teilhardina* species identified on the three northern continents (Ni *et al.* 2004; Smith *et al.* 2006; fig. 2).

4. Paleobiogeography of Paleocene/Eocene mammals

Several studies since Depéret (1908) have argued that mammals dispersed through Greenland to explain the similarities between North American and European faunas during the Early Eocene. The discovery of an early-middle Eocene subtropical fauna in the Eureka Sound Formation of Ellesmere Island, Canadian Arctic, at 79° of latitude confirms the warm conditions and the possibility of land bridges at high latitude (McKenna, 1983; Dawson 2001). The strong relationships between the earliest Eocene modern mammals of the Bighorn Basin, Wyoming and those of Dormaal, Belgium implicate that faunal exchanges between Europe and North America started from the time of the PETM. The primitive conditions of the modern mammal species of Dormaal in comparison to the more advanced species from Wyoming suggest that they migrated from Europe to North America (fig. 1). However, the presence of some typical North American late Paleocene genera in the Dormaal fauna such as Phenacodontidae, Nyctitheriidae, and Oxyaenidae also suggest a dispersal event from North America to Europe. Whatever the dispersal scenarios considered no modern mammal groups have been identified in Paleocene deposits of both Europe and North America with the exception of rodents and a few carnivoran specimens at the latest Paleocene.

The recently discovered Indian fauna of Vastan has important paleobiogeographic implications as it suggests much more exchanges with Europe than with Asia. This has probably to be explained with the paleogeography of the Tethys during the Early Eocene and the timing of the collision of the Indian subcontinent with Asia. Several Indian modern groups present primitive conditions and are represented by a high diversity suggesting that some modern groups such as bats and primates could originate in India. Unfortunately, earliest Eocene and Paleocene mammal faunas of India are still unknown.

The composition of the Eastern Asian faunas like those of China indicates more exchanges with North America than with Europe but this concerns mainly primitive groups that probably originated in Asia and migrated to North America via the Bering Strait by the time of the late Paleocene and/or early Eocene. However, the earliest Eocene fauna from the Lingcha Formation in South Chinese suggest a direct dispersal from Asia to Europe (fig. 1).

4. Conclusions

The geographic origin of modern placental mammals is not yet identified but recent studies and discoveries suggest South Asia as the dispersal center. The study of the microevolution of different modern mammal genera, as for example in the primate *Teilhardina* is particularly indicative of the fast mammal radiation and dispersal during the PETM. Due to this rapid evolution during this short period of time the isotopic analysis is complementary to the morphological study for inferring paleobiogeographic hypotheses.

The comparison of the early Eocene fossil records in Europe, North America, India and China indicates that the dispersal of modern mammals on the three northern continents could have happened in several waves. Up to now, there is no indication that all modern groups originated from a single area. Discovery of new Paleocene localities in South Asia, particularly in India would be necessary to elucidate this question.

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Figure captions

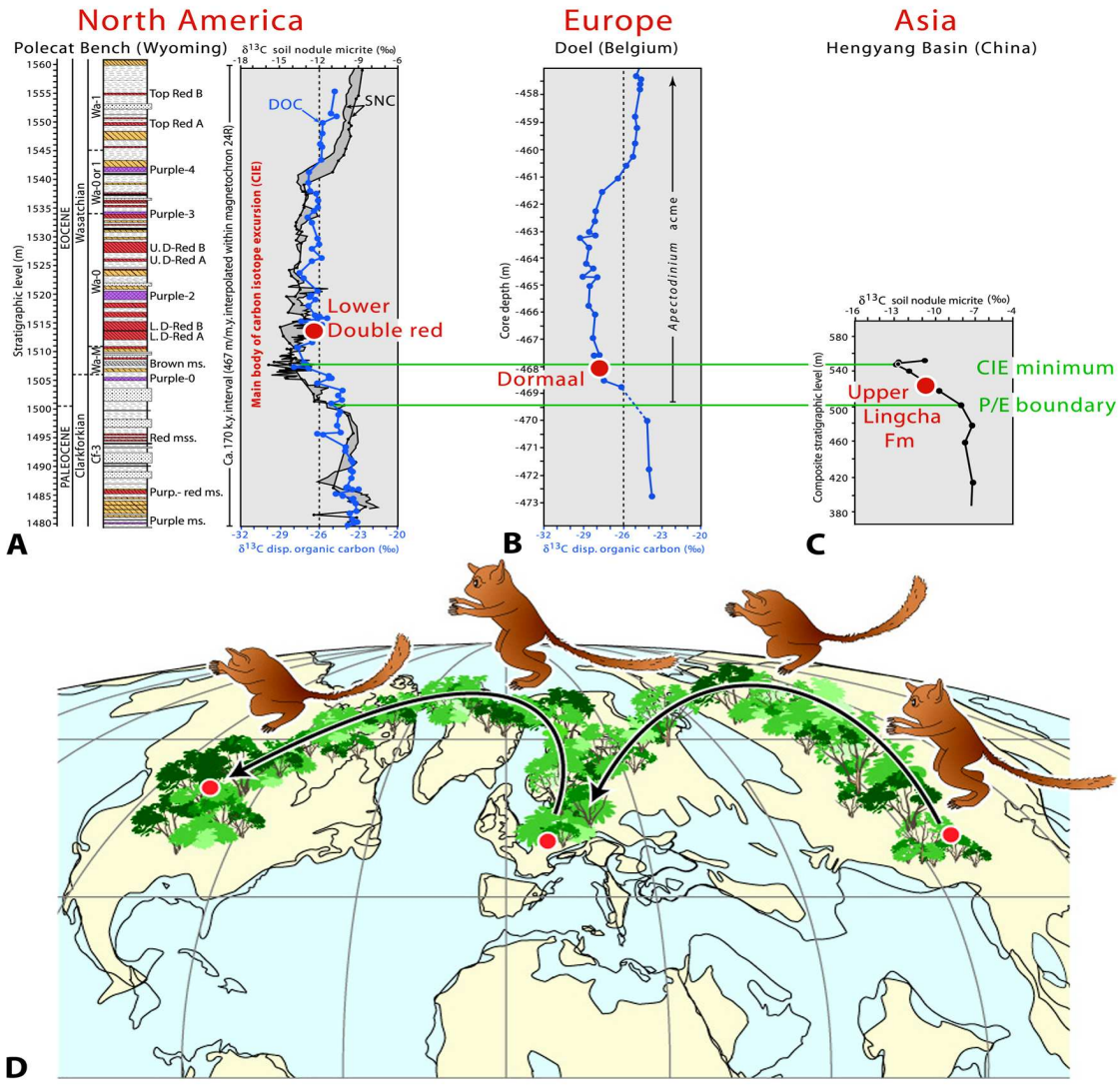

Fig. 1. – Paleogeographic map showing hypothetical migration routes of the earliest primate *Teilhardina* during the PETM at the earliest Eocene. Timing of migration is obtained by correlations of the $\delta^{13}C$ excursion in North America (A), Europe (B) and Asia (C). *Teilhardina* and other modern mammals first occur in the Lower Double Red (1512 m) of Polecat Bench, Wyoming, which is situated above the minimum value of the Carbon Isotope Excursion - CIE (spike at 1507 m). The Lower Double Red has an estimated age of 19-25 thousand years above the P/E boundary based on soil carbonate nodules (SNC) and dispersed organic carbon (DOC) (from Smith *et al.* 2006).

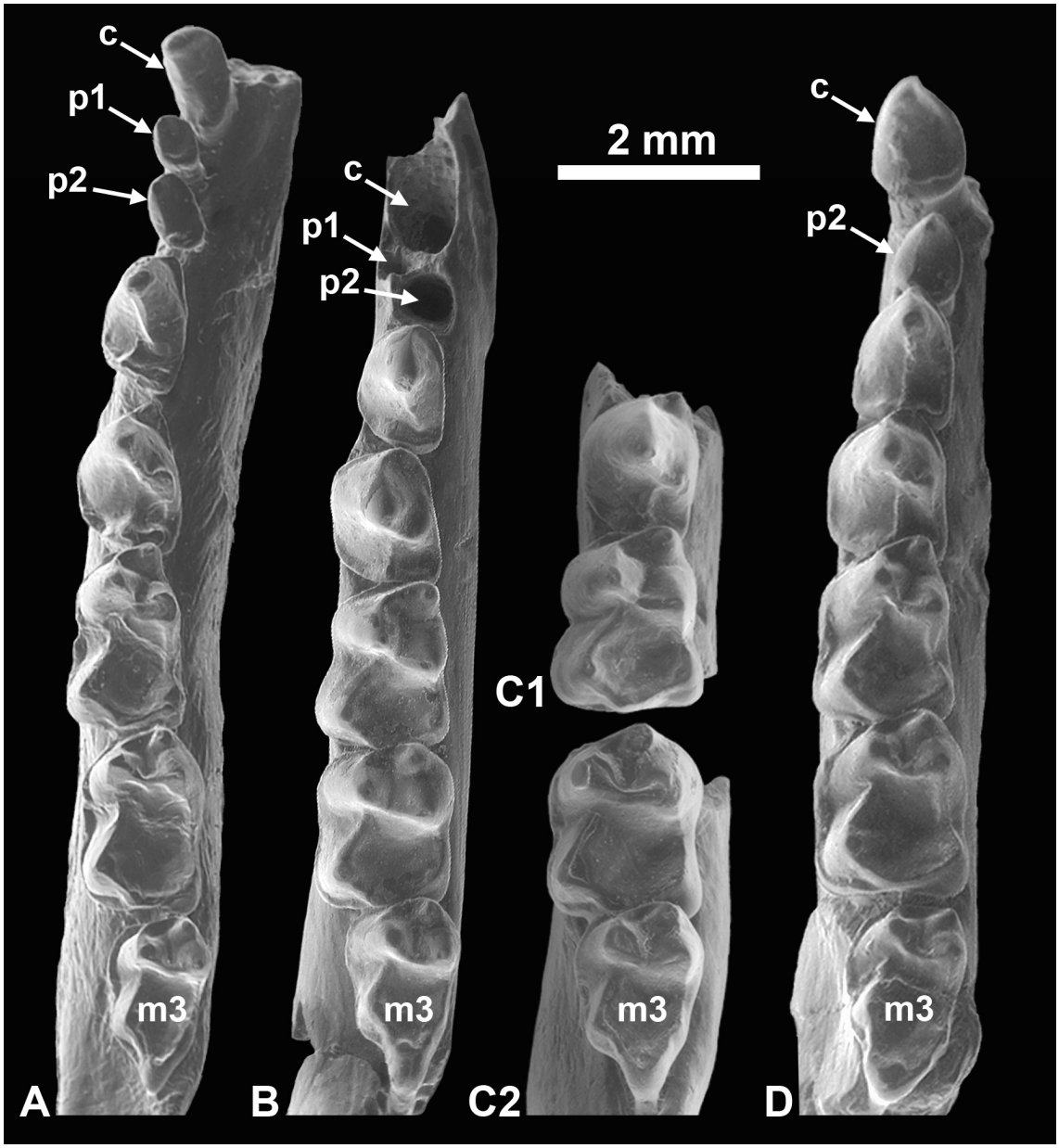

Fig. 2. – Lower teeth of earliest Eocene *Teilhardina* species (SEM in occlusal view): *T. asiatica* from China IVPP V12357 (A), *T. belgica* from Belgium IRSNB M64 (B), *T. brandti* from Wyoming USNM 493913 (C1, reversed), USNM 493914 (C2), *T. americana* from Wyoming USNM 493914 (D, reversed). Main morphological changes from *T. asiatica* to *T. americana* are: canine changes from caniniform to premolariform shaped, p1 reduces and disappears, m2 becomes square shaped, m3 hypoconulid lobe increases breadth (modified from Smith *et al.* 2006).

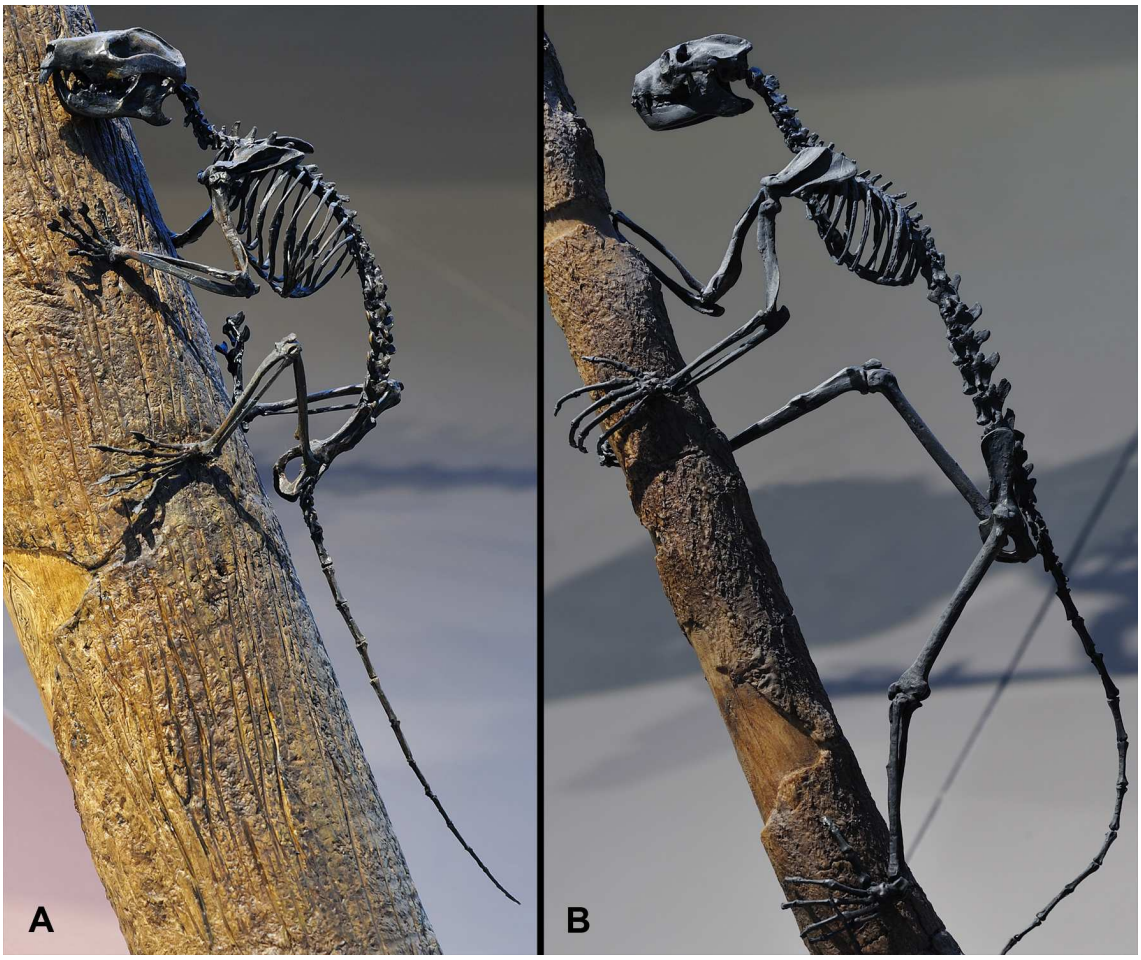

Fig. 3. – Plesiadapiform *Plesiadapis cookei* from Late Paleocene of Wyoming (A) and primate *Notharcthus tenebrosus* from Early Eocene of Wyoming (B). Plesiadapiforms were considered for long as ancestor of primates. Studies of nearly complete skeletons of plesiadapiformes and Early Eocene primates suggest that they are sister-groups or that their resemblance results from a convergent evolution. Primates have eyes in front with postorbital bar, nails, opposable thumb (hallux) and big toe (pollex), elongate tarsals (calcaneum and astragalus). Plesiadapiforms do not present these characters and have lateral eyes and claws.

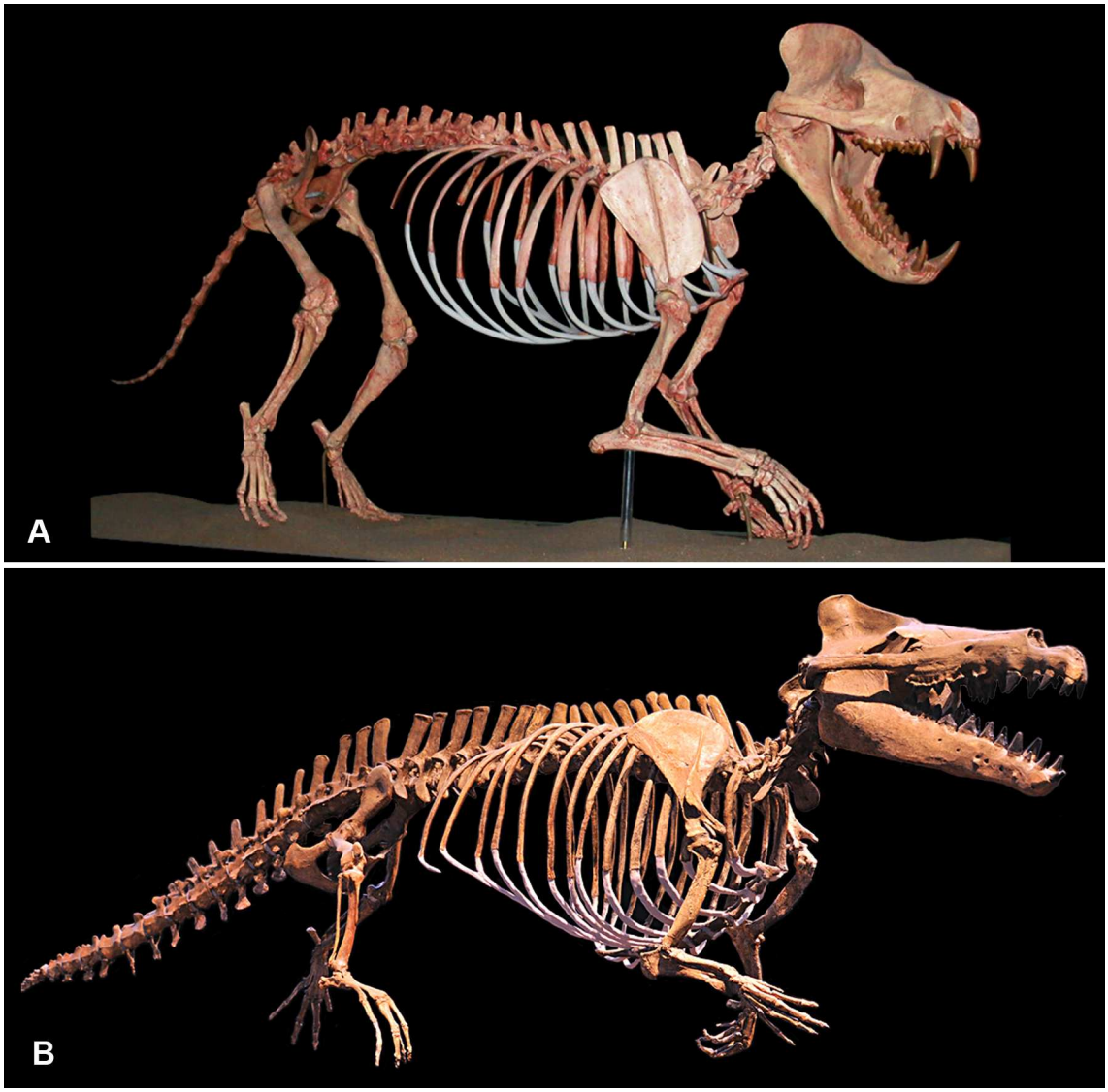

Fig. 4. – Mesonychian *Sinonyx jiashanensis* from Late Paleocene of China (A) and cetacean *Maiacetus inuus* from Middle Eocene of Pakistan (B). Mesonychians were considered for long as ancestors of cetaceans. Discovery of footbones of early whales allowed recognizing artiodactyls as ancestor or sister-group of cetaceans (Gingerich *et al.* 2001).