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Arguments for a mammalian and reptilian dispersal from Asia to Europe during the Paleocene-Eocene boundary interval

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The Paleocene-Eocene mammalian faunal turnover included the first appearance in northern regions of Eurasia and America of artiodactyls, perissodactyls, primates and hyaenodontids. An origin of these groups in Asia seems very probable (with the exception of hyaenodontids, of possible African origin). Dispersal of these groups is highly contentious, with recent assessments suggesting a dispersal from North America to Europe. The fossil evidence concerning these groups, including recent discoveries in eastern Asia, is reviewed. It confirms the presence in Europe of primitive sister-species or sister-genera of most of these North American newcomers, and emphasizes the absence of most of these genera in eastern Asia. More convincing evidence is found for turtles, with Geoemydinae and Carettochelyinae arriving in Europe from Asiatic origins, but not found in North America. On the whole, another scenario appears more likely: equoid perissodactyls, notharctid primates, the stem-artiodactyl *Diacodexis*, and hyaenodontids probably dispersed from western Asia to Europe first, at the same time as geoemydines, carettochelyines and several lizards. These mammals then dispersed to North America from Europe, whereas some of their relatives dispersed from their unknown province of origin to east Asia (and Isectolophidae probably from Asia to North America). Such a direct Asia to Europe dispersal was long dismissed because the Turgai Strait was believed to have acted as a barrier. However, new geological evidence suggests that the Turgai region allowed the dispersal of land vertebrates, possibly controlled by sea level falls and environmental changes.

Le renouvellement des faunes mammaliennes à proximité de la limite Paleocène-Eocène a inclus la première apparition dans les régions nordiques d'Eurasie et d'Amérique des artiodactyles, périsodactyles, primates et hyaenodontidés. Ces groupes ont très probablement une origine asiatique (à l'exception des hyaenodontidés, pour lesquels une origine africaine est également possible). La dispersion de ces groupes est débattue, avec plusieurs prises de position récentes en faveur d'une dispersion d'Amérique vers l'Europe. Les données fossiles concernant cette question sont ré-examinées. Elles confirment la présence en Europe de groupes-frères primitifs de la plupart de ces nouveaux arrivants nord-américains, et font ressortir l'absence de la plupart de ces genres dans l'est de l'Asie. Les tortues apportent un argument de poids, puisque les Geoemydinae et les Carettochelyinae arrivent, n'ont jamais été trouvées en Amérique du Nord et sont d'origine asiatique. Un autre scénario paraît plus probable: que les Equoidea, les primates notharctidés, *Diacodexis* et les hyaenodontidés sont allés d'abord de l'ouest asiatique à l'Europe, en même temps que les geoemydinés, les carettochelyinés et plusieurs lézards. Ces mêmes mammifères sont ensuite passés d'Europe en Amérique du Nord, alors que certains de leurs parents sont allés de leur province d'origine inconnue vers l'est asiatique (et les Isectolophidae probablement d'Asie en Amérique). Une telle dispersion directe d'Asie en Europe a longtemps été rejetée parce que le Détroit de Turgai aurait fait barrière, mais de nouvelles données géologiques suggèrent que la région de Turgai a permis le passage de vertébrés terrestres, sous contrôle des baisses du niveau

marin et des modifications de l'environnement.

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INTRODUCTION

The Paleocene-Eocene boundary interval in Europe is well known for the remarkable faunal turnover, which affected, among others, the mammalian and reptilian faunas. Because an official limit for the Paleocene-Eocene boundary has not yet been chosen, we will use the European Land Mammal Ages Cernaysian and Neustrian to refer to 'typical Paleocene' faunas (Cernaysian) and 'typical Eocene' (Neustrian) faunas. These Ages are based on the mammalian faunas under consideration here, whereas the correlations between these faunas, the continental beds that yield them, the marine geological stages, and the major geological and climatological events of the boundary interval are variably understood (see contributions in Aubry *et al.* 1998, Schmitz *et al.* 2000). In Europe, the broad picture of the Cernaysian-Neustrian turnover is well known. This turnover has been recognized earlier, as e.g. the 'grande coupure hyracothérienne' of Depéret, but it was much more completely described following a later and considerable increase in our knowledge of these faunas (Russell 1964, 1968, 1975, Broin 1977, Buffetaut 1985, Augé 1993, Lapparent de Broin 2001). Recent overall treatments of the mammals and turtles can be found in Hooker (1998) and Hutchison (1998), respectively. In any case, many details of the chronology and correlations of this turnover are still unclear. In this paper we give details about mammals and turtles, and we will only briefly allude to other elements of the herpetofaunas.

Cernaysian mammalian faunas of the Paris Basin and Germany are dominated by multituberculates, Arctocyonia, Condylarthra (Meniscotheriidae, Hyopsodontidae - including many endemic Louisininae, Tricuspidontidae), and Plesiadapiformes, which were earlier considered as archaic primates (Plesiadapidae, Saxonellidae, Toliapinidae). These faunas also contain less abundant mesonychids (Mesonychia), several groups of Lipotyphla and primitive insectivore-like families (Palaeoryctidae, Leptictidae, Pantolestidae, ?Mixodectidae; all these are sometimes included in Proteutheria, or variously spread into controversial orders). Several micromammals were recently added to the Cernaysian fauna, possibly documenting a level more elevated than Cernay and Berru within the Cernaysian (Lopez-Martinez & Pelaez-Campomanes 1999). Cernaysian reptilian faunas include, among others, champsosaurs (Choristodera) and a depauperate squamate fauna (Rage & Augé 1993). Turtles are represented by *Compsemys* (otherwise restricted to North America), Trionychidae, some 'chelydroid-looking' species, and two indeterminate endemic taxa of Cretaceous Eurasian affinity. Crocodiles are represented by *Allognathosuchus* (of North American affinity), *Diplocynodon* and *Asiatosuchus*.

Neustrian faunas (formerly called 'Sparnacian') contain some survivors of the preceding fauna, and a wealth of newcomers. The number of mammalian genera crossing the boundary has increased from six (Russell

1980) to nine (Smith 1997, Godinot 1998). One more turtle, a 'chelydroid' found at Le Quesnoy (Nel *et al.* 1999) also crosses the boundary, but we cannot confirm that *Compsemys* did (this genus was listed in the Dormaal fauna in Godinot *et al.* 1978, but no definitive *Compsemys* material is actually found in the Dormaal sample). Moreover, the condylarth *Paschatherium* remained the dominant micromammal in the Dormaal fauna, and the plesiadapid (*Plesiadapis-Platychoerops* lineage) remained the dominant mammal in the Le Quesnoy fauna (Nel *et al.* 1999). These elements render the turn-over somewhat less abrupt than before, and give important information concerning possible hiatuses in the succession of faunas.

The wave of Neustrian immigrants includes many reptiles, among which are Testudinidae, Geoemydinae, Carettochelyidae, pleurodire turtles (Podocnemididae), Iguanidae, Agamidae, Helodermatidae, Gekkonidae, etc. (Augé 1993, Rage & Augé 1993, Augé *et al.* 1997). In the wave of mammalian immigrants, two groups can be distinguished. The first group contains all the genera of probable North American origin, because they are known in the Clarkforkian or earlier: apatemyids, phenacodontids, paromomyids, miacid carnivores, and oxyaenid creodonts. To these can be added taxa of Asian origin, which dispersed from Asia to North America at the Tiffanian-Clarkforkian boundary: Rodentia, coryphodontid Pantodonta, and esthonychid Tillodontia. All these are thought to have dispersed from North America to Europe at the Clarkforkian-Wasatchian boundary, and this is quite a consensual view. Here, we do not review all the new Neustrian taxa, some of which are special cases: marsupials, Plagiomenidae, Taeniodonta, and bats (see Hooker 1998). The second group contains genera of the modern orders primates, perisodactyls, artiodactyls, and the hyaenodontid creodonts. These also show up for the first time in North America at the Clarkforkian-Wasatchian boundary, coming from elsewhere.

Their origin has been the subject of much debate. A comprehensive review of this problem was given by Krause & Maas (1990). In this review, they concluded that the origin had to be either in Africa or in India, and they developed for the first time the idea that these four groups might have evolved on India during its Paleocene move toward the north, and disembarked in Asia at the moment of the collision, close to the Paleocene-Eocene boundary, subsequently dispersing through Holarctica. Continuing discoveries in Asia led to a more recent analysis of the role of Asia in the origin of many modern orders of mammals (Beard 1998). Emphasizing this role, Beard concluded that these four groups originated in Asia, and were one among a series of dispersal waves of Asian taxa which, during Paleocene and Eocene times, successively colonized North America. These four groups then dispersed from North America to Europe, a conclusion firmly restated by Beard & Dawson (1999). We propose to have another look at the recent discoveries to see if this dispersal model is as straightforward as presented in these latter papers, and we add information from turtles and other reptiles, which were not taken into account in this debate previously. Before this evidence is discussed, problems of geological correlations and paleogeography need to be briefly considered.

GEOLOGICAL CORRELATIONS

The dispersal between North America and Europe has been linked with geological correlations. When the Sparnacian deposits containing Neustrian mammals were, on the basis of evolutionary grades in plesiadapids, partly correlated with the Clarkforkian (Gingerich 1976, Rose 1981, Springhorn 1984), the dispersal had to be from Europe to North America (Hooker 1980 for '*Hyracotherium*'). Likewise, the recognition of some Neustrian mammals as being more primitive than their earliest Wasatchian relatives would also imply this Europe to America dispersal

(Godinot 1981, 1982, 1996, Estravis & Russell 1989, Hooker 1994). However, having studied the new Wasatchian 0 fauna, Gingerich (1989) concluded that these newly discovered mammals were more primitive than their Sparnacian relatives, which implied a dispersal to North America first, and then from there to Europe. Confronted with these contentious opinions, Krause and Maas (1990) emphasized the consideration of mammalian faunal similarity, which led to a return to a grade- and time-equivalence between earliest Wasatchian and earliest Neustrian mammals, in which case it seems logical to assume all European newcomers arrived with the other North American invaders (Krause & Maas 1990, Beard & Dawson 1999). A clear and definitive answer should be attainable. However, the European mammalian record is still neither as rich nor as continuous as the North American one, and also less thoroughly studied. This situation is improving with the renewed study of the Dormaal fauna (Smith 1997, 2000), and with the study of new faunas (Antunes *et al.* 1987, Godinot *et al.* 1987, Marandat 1991, Estravis 1994, 2000, Nel *et al.* 1999). Some aspects of this new evidence will be discussed below.

Paleontological interpretations having been disputed, any other kind of geological evidence would be welcome. In this context, the location of the characteristic carbon isotope excursion in the North American record, at the base of the Wasatchian interval, is very promising (Koch *et al.* 1992). This excursion was subsequently identified within the Sparnacian Argile Plastique series (Thiry *et al.* 1998). However, these Argiles Plastiques are clay deposited in a lake, and are not directly correlated with mammal-bearing Sparnacian deposits. Indirect correlation of the Meudon section with the Argile Plastique suggests a relatively late age for the Meudon fauna, a result in agreement with the content of the fauna (Hooker 1996). The recognition of the carbon isotope excursion in the Provence Basin allowed the placement of the Palette fauna above the excursion (Cojan *et*

al. 2000). However, the Palette fauna is not rich and cannot be precisely correlated with Paris Basin faunas. Recently, a new geological correlation was proposed for the Dormaal Sands, which lie at the bottom of the Tienen Formation (formerly 'Upper Landenian', Steurbaut *et al.* 1999). Correlation of these sands with more complete successions in several boreholes led to the placement of the Dormaal sand below a recognizable kaolinite influx in the Tienen deposits. This influx is interpreted through correlation with the Cap d'Ailly section as laying below the carbon isotope excursion (Steurbaut *et al.* 1999, 2000).

Through these correlations, the Dormaal fauna, which is the European reference-level MP7, appears older than the Wasatchian 0 fauna. Using the chronostratigraphic framework of Berggren & Aubry (1998), with the carbon isotope excursion at 55.5 Ma, an age for the burial of Dormaal mammals is given at 55.8 by Steurbaut *et al.* (2000), and between 55.8 and 55.5 by Smith (2000). If these correlations hold, they confirm the opinion of those who considered earliest Neustrian ('Sparnacian') mammals to be older than their earliest Wasatchian relatives. (For an opposing view based on sequence stratigraphy, see Beard & Dawson 2001.)

The correlations between the Asiatic faunas and those of North America and Europe have been controversial (see e.g. Beard 1998, Lucas 1998). However, they have greatly improved. In spite of mammals being excellent biochronological tools, the Asiatic faunas are still neither numerous nor rich enough to be unambiguously correlated with the continuous North American mammalian record. The most common view correlated Gashatan with Clarkforkian, and Bumbanian with Wasatchian (Dashzeveg 1988, Meng *et al.* 1998, Ting 1998, Wang *et al.* 1998). It received strong confirmation from a detailed study of the Lingcha Formation, Hunan, China, which showed a Bumbanian fauna to lie just at and above the carbon isotope excursion (Bowen *et al.* 2002). However, the Gashatan-

Bumbanian boundary is not yet precisely located, being either equivalent to the Clarkforkian-Wasatchian boundary, or older. This Asiatic correlation cannot yet be extended to Europe. It should be recalled that there are much fewer genera in common between the Asiatic Bumbanian and the Wasatchian than there are between Wasatchian and Neustrian: a smaller number of lineages are available for correlation. The close correlations that are sought here will become more secure only when more genera in common can be studied in detail, or when the carbon isotope excursion can be located in a larger number of sections.

PALEOGEOGRAPHY

It is difficult to find paleogeographic reconstructions of the whole Eurasian landmass around 55 Ma. Multidisciplinary efforts have been devoted to synthesizing information around the Tethys from Spain to the Aral Sea on the northern side, and from Morocco to Arabia on the southern side. Dercourt *et al.* (1993) gave paleogeographic maps for the late Maastrichtian and the Lutetian. More recently (Dercourt *et al.* 2000), a map of the early-middle Ypresian (55-51 Ma) extends from Spain to the Aral Sea. This map shows quite well the limits of land and sea on the western part, and on the eastern part from the Black Sea and Ukraine to the Ural region; however, a southern coastline is not given between the south of France and Romania-Bulgaria-Greece. The geological, especially tectonic, history of the Alpine and Carpathian regions is relatively well known. However, it is very complex and does not always include information about the terrestrial or marine status of the microplates. As a result, mapping was not included (Meulenkamp *et al.* 2000). In what concerns terrestrial areas and mammalian dispersal into Eurasia, the problems are simplified by the fact that the northern parts of this landmass were little affected by the Alpine movements. A broadly continuous landmass is permanently present, interrupted only by epicontinental seas.

A potential barrier to mammalian dispersal was the Polish lowland basin, possibly prolonged to the Dniepr-Donetz marine basin. However, the connection between these basins is conjectural, not being mapped by Meulenkamp *et al.* (2000). Moreover, the Polish lowland basin is filled with continental deposits; it should not have been an obstacle for mammalian dispersal. The most important barrier, which has often been considered as the permanent barrier preventing any direct mammalian dispersal between Asia and Europe (McKenna 1975, 1983), is the epicontinental Siberian Sea, which was supposed to connect the Arctic Ocean with the Tethys through the Turgai Strait (Fig. 1). However, some authors maintained dispersal possibilities across this region (e.g. Savage & Russell 1983). (The Siberian Sea has been repeatedly called 'Obik Sea' by mammalian paleontologists, but this term seems inappropriate and is not used by Russian scientists.) On the paleogeographical maps of Smith *et al.* (1994), the Siberian Sea and Turgai Strait are a continuous major seaway on the Ypresian map (53 Ma), but it was not a continuous seaway during the Paleocene. On the 60 Ma map, communication with the Arctic Sea seems absent or very tenuous, and in the south a large land area isolates the Siberian Sea from the Tethys. The timing of the transgression in this region is critical for us, and recent and continuing work gives important new results. Correlations with Western European chronology through dinoflagellates (Iakovleva 2000) allowed the placement of an erosional unconformity between the Paleocene Kirshorskaya Formation and the Eocene Voravogskaya Formation, in a borehole from the western margin of the Polar Urals (Oreshkina 2000). This implies an emersion in that northwestern Ural region. A short hiatus appears in the dinoflagellate zonation of Iakovleva *et al.* (2000), who studied sections from the Petchora depression and the Turgai Strait. This hiatus again suggests an emersion.

A more extensive work shows that the Turgai Strait was flooded close to 57 Ma, and

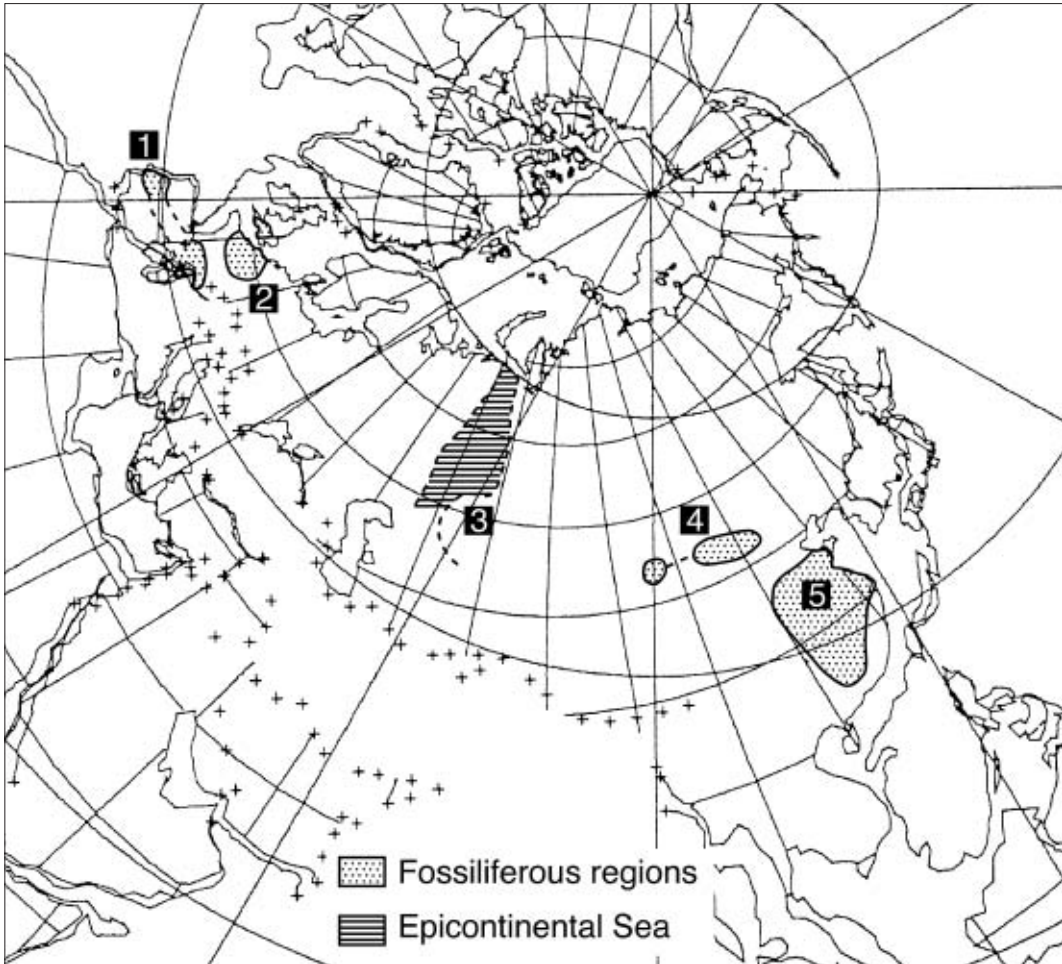


Figure 1 The Eurasian landmass as broadly reconstructed in north polar stereographic view at 60 Ma by Smith & Briden (1977). It shows how far apart the two main fossiliferous regions are, southwestern Europe (1) and Anglo-Belgian-Parisian Basin (2) on one side, and Mongolian Plateau-Sinkiang (4) and eastern China (5) on the other side. Large areas in between are not sampled. The epicontinental sea in the Ural / Ob region is the Siberian Sea, connected to the Arctic Ocean, terminating in the south by the Turgai Strait (3), a seaway not permanently connected to the Tethys (Iakovleva *et al.* 2001).

it allows the recognition of a series of transgressive cycles correlated with Western European cycles (Iakovleva *et al.* 2001). More importantly, this study confirms the continuity of the Siberian Sea with the Arctic Ocean and North Sea, but it does not provide clear evidence of continuity with the Tethys. On the contrary, a temporally short interval of Tethyan influence in their record suggests to these authors that the Turgai Strait was a region of migrating terrestrial biotas during intervals of major sea level fall (Iakovleva *et*

al. 2001). This new and better-calibrated evidence is important: it clearly suggests the possibility of terrestrial faunal dispersal across the Turgai Strait, probably mediated by both climate and sea level changes.

ANOTHER LOOK AT THE MAMMALIAN FOSSIL EVIDENCE

Because four mammalian taxa (Primates, Perissodactyla, Artiodactyla, and Hyaenodontidae) appear precisely at the same time in the well documented North American record



Figure 2 Lower m3 of early Eocene European notharctids. **a:** *Donrussellia provincialis* from Rians; **b:** *D. (Palettia) magna* from Palette; **c:** *Cantius* sp. from Le Quesnoy. Early *Cantius* has derived characters in comparison with *Donrussellia*, e.g. a broader and lower trigonid, a much lower protocristid, and the paraconid smaller and closer to the tip of the metaconid. *Cantius* reached North America, but *Donrussellia* did not. Scanning electron micrographs of casts. Bar = 1 mm.

at the Clarkforkian-Wasatchian boundary, they are suspected of sharing a common origin and dispersal route, and they have been often treated together. The consensual idea is that they originated in a tropical area and dispersed during the global warming episode included in the series of Paleocene-Eocene boundary events.

The place of origin of Primates seems to us relatively clear. We concur with Beard (1998) that they have their closest living sister-groups, Tupaiidae and eventually Galeopithecidae, surviving in southeast Asia. *Tarsius* also testifies to early Asiatic dichotomies in primate phylogeny (the other alternative would be Africa, e.g. Gingerich 1986, 1989, Gheerbrant 1998). Thus, Primates probably originated in Asia (contra the opinion adopted in Godinot *et al.* 1987). However, their dispersal history is not at all clear. They must have reached Africa very early, during the Paleocene (Sigé *et al.* 1990). The primates who show up at the Cernaysian-Neustrian and Clarkforkian-Wasatchian boundaries pertain to the same families Omomyidae and Notharctidae. The genera *Teilhardina* and *Cantius* are found on both sides of the Atlantic. However, the genus *Donrussellia*, which is widely recognized as the primitive sister-group of *Cantius*, is found in Europe but not in North America. This is in our opinion quite a strong argument in favour of dispersal from Europe to North America. The

other alternatives would be either that *Donrussellia* came also through America but without leaving descendants there, or that this genus is in fact derived from *Cantius* (Gingerich 1986). This latter view seems at odds with the common trend toward larger sizes at the time of initial radiation of these genera (Fig. 2), and arguments against it were given (Godinot 1992, Rose *et al.* 1994). If we look at the discoveries in Asia, the Mongolian *Altanius* is an omomyid, a primitive primate, or a plesiadapiform (Dashzeveg & McKenna 1977, Rose *et al.* 1994). The Shang-Huang fissure fillings added a wealth of new middle Eocene primates from eastern Asia, including eosimiids, tarsiids, and adapids (Beard *et al.* 1994). Other discoveries also came from basin deposits. However, in all these new discoveries, not one notharctid was found. If *Teilhardina* and *Cantius* had dispersed through Beringia, why are no notharctines found yet in those parts of east Asia which accommodated primates? Of course the fossil record of primates in Asia is still very incomplete. However, the more primate discoveries in eastern Asia, the more surprising is the absence of a notharctine radiation there. This suggests to us that they may have inhabited other parts of Asia and dispersed at its western side toward Europe. Both *Donrussellia* and *Cantius* seem to have reached Europe, with only *Cantius* continuing toward North America (Fig. 4).

The case of artiodactyls is relatively similar to that of the primates. Most authors agree that artiodactyls, for many reasons including their close relationship with the clearly Asiatic Mesonychia and Cetacea, originated on the Asiatic continent. Strangely, the most primitive artiodactyls known at present are species of the genus *Diacodexis*, which are at the root of the European and North-American Eocene artiodactyl radiations. Beard (1998) even concurs that the European species of *Diacodexis* are more primitive than the North American Wasatchian ones, something that suggests to us a Europe-to-America dispersal. The only *Diacodexis* found in Asia is '*D.*' *pakistanensis*, considered by some as the most primitive species of the genus (Thewissen *et al.* 1983; Thewissen & Hussain 1990; Beard 1998). However, this relatively late species is quite different from the others. We concur with Hooker (1998) that it is in fact dentally more derived than the other species, and we agree with Sudre (pers. comm. 1996), as was suspected by Thewissen *et al.* (1983), that it should be placed in a different genus.

Anyway, what is interesting to us is that a close relative of *Diacodexis* is found in a relatively western part of Asia, whereas no such primitive artiodactyl has been found until now in the eastern part. We find it very strange, knowing how later artiodactyls adapted well to more open or arid environments, that none was found until now in the many faunas of the Mongolian Plateau before the Irindinmanhan (Meng & McKenna 1998). Beard (1998) used the evidence of the new Wutu artiodactyl, apparently a very small and primitive suiform (Tong & Wang 1998), in favour of his 'East of Asia' dispersal model. However, the Wutu suiform does not seem dentally clearly more primitive than *Diacodexis*; on the contrary e.g. the m3 talonid is more extended and more complex. As *Diacodexis* dentally resembles the arctocyonid ancestors of artiodactyls (Rose 1996), suiforms must have gone through a '*Diacodexis* dental stage', as did the more bunodont artiodactyls, which evolved from *Diacodexis* in

Europe and in North America (Krishtalka & Stucky 1985, Sudre & Erfurt 1996). This evolution could have taken place earlier in Asia, due to the primitive postcranial characters retained by suiforms; however, if some '*D.*' *pakistanensis* had retained enough primitive postcranial characters, the evolution of suiform teeth might have been a relatively late change. In fact, '*D.*' *pakistanensis* retains primitive postcranial characters (Thewissen & Hussain 1990), and because suiforms share the peculiar artiodactyl astragalus, they have to be descended from very cursorial forms. The remarkable Wutu suiform might well not be the oldest artiodactyl.

In any case, this taxon accentuates the provinciality and dissemblance of eastern Asiatic faunas with those of Europe and North America. Again, one can think of *Diacodexis* (never found in eastern Asia and without close relatives on the Mongolian Plateau) as a southern or western Asiatic taxon that dispersed westward. Relatives of the Wutu suiform may have later reached the Mongolian Plateau (Helohyidae), and also dispersed on other continents (Fig. 4). It also should be recalled that in Europe, several lineages of *Diacodexis* were differentiated early and that some species, especially *D. antunesi* from Silveirinha but also *D. gigasei* from Dormaal, are more primitive than the earliest Wasatchian *D. ilicis*, strongly supporting a Europe to America dispersal of this genus (Estravis & Russell 1989, Smith *et al.* 1996).

The case of perissodactyls is a complex one. Origin in Asia seems to us very probable. Proponents of an African origin argue from their eventual sister-relationship with Hyracoidea (Fisher 1986, Gingerich 1989); however, such a relationship is contradicted by both the morphological and the molecular evidence favouring the inclusion of hyracoids in the Paenungulata (e.g. Novacek 1990), a view that we support due to the structure of the hyracoid tarsus (Godinot *et al.* 1996). An origin of Perissodactyla outside of tethytheres or Afrotheria is likely. In these conditions, the fossil record of early perissodactyl diver-

sity in Asia strongly points toward an Asiatic origin (e.g. Beard 1998, Hooker 1998).

What about dispersal out of Asia? From the study of some early '*Hyracotherium*' from Rians, a Europe-to-America dispersal had been proposed (Godinot 1981). However, from the study of the new Wasatchian 0 fauna, Gingerich (1989) concluded that his hyracotheriines were more primitive. From a subsequent detailed phylogenetic analysis of the earliest representatives of the order, Hooker (1994) concluded that the primitive sister-groups of the Wasatchian immigrants were found in Europe, thus confirming a Europe to America dispersal, and consequently an earlier Asia to Europe dispersal (Hooker 1998). Nonetheless, Beard (1998) claimed that perissodactyls had to follow his Beringian eastward model, and an Asia to Europe dispersal was again excluded (Beard & Dawson 1999).

A detailed reappraisal of the earliest perissodactyls is beyond the scope of this paper. However, new discoveries in Asia will be mentioned. The only Gashatan perissodactyl, questionably found in the Bayan Ulan fauna, is distinct from the earliest Euramerican genera and *Orientalophus* (Meng *et al.* 1998). This form is closer to a Wutu genus, and the Wutu perissodactyls include an isctolophid, an eomorpid, and a ?lophialetid (Tong & Wang 1998). These early east Asiatic faunas document some typically Asiatic groups, but do not document until now the *Cymbalophus*-'*Hyracotherium*' group, i.e. the equoids, which shows up in Europe and America at Paleocene-Eocene boundary times. One interpretation is that the earliest equoids came from western Asia to Europe, and then to North America. The early perissodactyl evolution must have been complex, and the differentiation of many families must have occurred in Asia prior to their dispersal on other continents. For example, a later dispersal of Eomoropidae and Brontotheridae from Asia to America is well documented. A dispersal of Lophiodontidae from Asia to Europe seems also inescapable, either relatively early

if *Lophiaspis* is considered a lophiodontid, or later in the Cuisian if *Lophiodon* is the first representative.

In any case, some direct Asia-to-Europe dispersal seems to have occurred. Perissodactyls must have had an early history on the immense Asiatic landmass, including some provincialism and geographical differentiation. Whereas some later dispersals certainly occurred directly from Asia to America, and a subcontemporaneous dispersal of isctolophids probably occurred from Asia to America, the early dispersal of Neustrian-Wasatchian equoids may well have been from western Asia to Europe. Such a scheme fits the phylogenetic analyses of Hooker (1994), is not contradicted by recent discoveries in eastern Asia, and is made possible by the similar dispersal of lophiodontids. A detailed phylogenetic study of the new east Asiatic perissodactyls undoubtedly will shed some light on this question.

The last of the four groups under scrutiny here is the family Hyaenodontidae. The geographical origin of this taxon is more problematic. Whereas Beard (1998) favours an Asiatic origin, Gingerich (1989) defends an African one. The interpretation of Paleocene fragmentary fossils from Morocco as hyaenodontids (Gheerbrant 1995, Gheerbrant *et al.* 1998) is now corroborated by better material from the same genus (Gheerbrant pers. comm. 2002, confirming the African origin proposed in Gheerbrant 1990, 1998). In spite of his own emphasis about phylogeny reconstruction being first, and biogeographical scenarios being 'contingent on them', Beard (1998) had no hesitation in relying on the fossil record to affirm an Asiatic origin for this family: a species of *Prolimnocyon* is described from the Bayan Ulan Gashatan fauna (Meng *et al.* 1998). This fossil "supports an Asian origin for... Hyaenodontidae" (Beard 1998, p. 26). In this case, hyaenodontids also would conform to the Beringian Asia-America scheme.

Is the picture so simple? It is remarkable that, on the cladogram of Beard (1998), based

on the work of Polly (1996), the European genus *Proviverra* appears as the most primitive branch. In the Dormaal fauna, four hyaenodontids are listed, including *Prolimnocyon* and *Arfia* (Smith & Smith 1996). A careful study of the apparently cosmopolitan genus *Prolimnocyon* will be exciting. Occurrence of this genus in a Gashatan fauna is not necessarily a proof of Asiatic origin for the clade. If the correlations of Dormaal mentioned above are exact, the Dormaal *Prolimnocyon* would be a late Gashatan equivalent. More numerous hyaenodontids and the presence of *Proviverra* in Europe could be explained by an origin in western Asia or Africa and subsequent dispersal to eastern Asia on one side, and to Europe and North America on the other side. Careful study of the most primitive hyaenodontid species should help clarify a probably complex history. The very small species *Proviverra eisenmanni* from Rians (Godinot 1981) is smaller than *Prolimnocyon chowi* from Bayan Ulan (Meng *et al.* 1998), and it presents characters that are likely primitive, e.g., a markedly labial orientation of the metastyle on its upper molars. The Rians fauna is probably younger than was thought when it was first studied (Escarguel 1999), however it contains primitive species and genera (*Donrussellia*), which testify to the presence of primitive lineages in southern France in the early Eocene. Importantly, the creodonts of Dormaal have just been revised and compared in detail with their Wasatchian 0 relatives (Smith & Smith 2001). These authors show that the four species of Dormaal Hyaenodontinae are the most primitive known so far, suggesting that they are ancestral to, or primitive sister-lineages of, the earliest Wasatchian 0 species (Smith & Smith 2001). This again considerably strengthens the view of a Europe-to-America early Wasatchian dispersal. Also in this case, there is more similarity between Neustrian and Wasatchian genera than there is until now between Wasatchian and Gashatan-Bumbanian ones. On the whole, a scenario of origin in Africa or western/southern Asia is likely,

followed by dispersal to Europe and then to North America, with persistence in Europe of primitive sister-groups (primitive sister-species of migrants, as in *Prolimnocyon* and *Arfia*, or primitive non-migrants such as *Proviverra*).

In summary, the geographic occurrence of families and genera of primates, artiodactyls, perissodactyls and hyaenodontids does not clearly show an east Asiatic and Beringian dispersal to North America at the Clark-forkian-Wasatchian boundary. Dispersals should be traceable at the generic and specific levels. Following his revision of the Dormaal fauna, Smith (2000) lists 37 genera, 22 of which are also found in North America. This shows that, close to a major dispersal event, many genera can be compared between the two related continents. In our case, this includes genera of clear North American origin (see above), whereas genera like *Cantius*, *Teilhardina*, *Prolimnocyon*, ‘*Hyracotherium*’, and *Diacodexis* are newcomers on both continents. If they had come from Asia through Beringia, why are they not more commonly found in eastern Asiatic faunas? Is the Asiatic fossil record, in spite of recent improvements, still so incomplete that a similar close faunal similarity would not yet have been sampled in eastern Asia? Based on the occurrences discussed above, we reassess the hypothesis of a western Asia to Europe dispersal, followed by a Europe to North America dispersal, which left in Europe some of the primitive sister-lineages (*Donrussellia*, *Proviverra*).

THE TURTLE EVIDENCE

The early Eocene European non-marine turtle fauna is partly undetermined at the genus and species level, because most specimens are not complete enough. However, it is always possible to identify the group to which the fossils pertain at the subfamily or ‘broad genus’ level (genus *sensu lato*; genera that would be split after revision of appropriate material). Contrary to mammals, there is no turtle genus common to Europe and North America in the early Eocene immigrants. The new turtles,

which arrived in the early Neustrian, had to come through a route other than North America.

Fresh water Testudinidae (including ‘Emyridae *sensu lato*’ of Hutchison) appear in the Paleocene of Anhui and Guangdong (Yeh 1974, 1979). *Elkemys australis* is the likely sister-group of all the fresh water testudinid turtles. *Anhuichelys* has possible phylogenetic relationships with North American as well as European taxa. *Hokouchelys* probably has close relationships with early Eocene Geoemydinae from France. In the Eocene, other taxa are reported in China, which have no special relationships with European and North American forms: they postdate the diversification of the subfamily. Unnamed fresh water testudinids (‘large headed’ Emydid n. gen. or ‘macrocephalic’ emydid, *Echmatemys*-like emydid, Emydid C) were mentioned from the Paleocene of

North America (Bartels 1980, Hutchison 1980, 1998). From what is written and figured about them, we can exclude any close relationship with the European forms. Those forms, which diversified after the early Wasatchian (including ‘Emydid P, E’ of Hutchison), are from their description, illustration, and our observations, unknown in Europe (Hay 1908, Hutchison 1980, 1992, 1998, Estes & Hutchison 1980, West & Hutchison 1981, Holroyd *et al.* 2001, Gunnell & Bartels 2001).

Some, such as the *Echmatemys* group, might nevertheless share with them an earlier common ancestor such as e.g. *Anhuichelys*. The genus ‘*Echmatemys*’ is for us heterogeneous: it should be split into several genera; and it has no close affinity with European *Palaeochelys sensu lato*. It could share a common Asiatic ancestor with the *Geiselmys-Ptychogaster* group, as shown by the

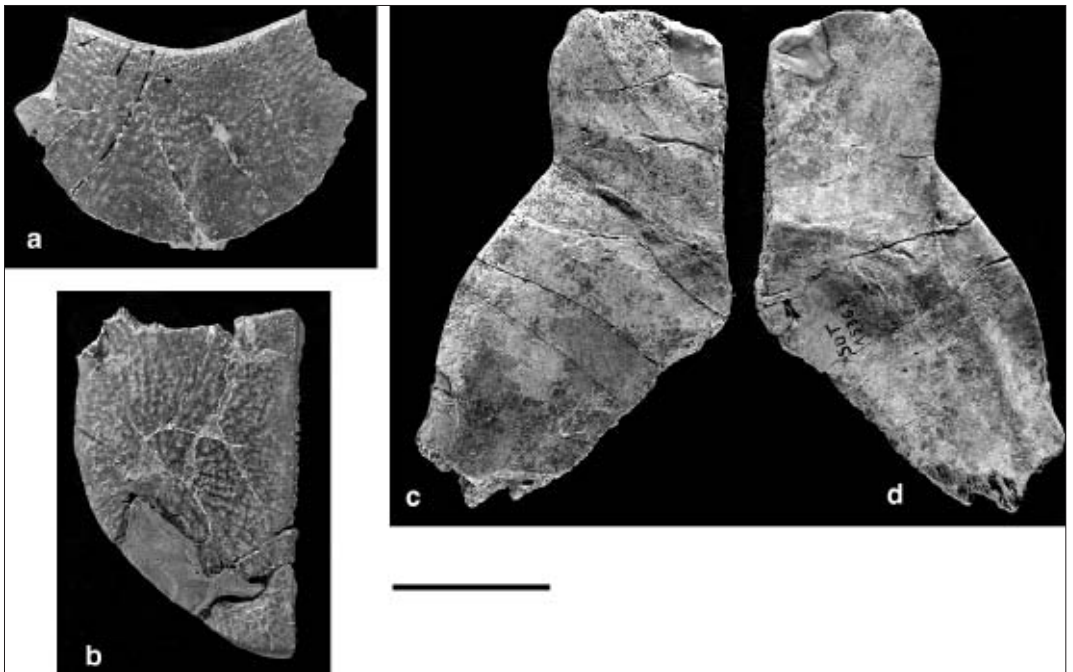


Figure 3 Early Eocene European turtles of a direct Asiatic origin. Eastern Paris basin, Mame Department, France, MNHN coll.; a,b: *Allaeochelys* sp., *Carettochelyinae* from Ay, Neustrian fauna, early Ypresian ("Spamacian"), MP8-9; **a**: ALx, nuchal, dorsal view (carettochelyine because of the coarse pitted-undulated decoration and absence of dermal sulci); **b**: AL 9218, right xiphiplastron, ventral view (carettochelyine because of the coarse pitted-undulated decoration and the particular width of the posterior lobe). **c,d**: ‘*Hadrianus*’ s. l. sp., terrestrial Testudinidae from Sables à Unios et Térédines Formation, Cuisian, MPI0, new coll. SUT, right epi-plastron, ventral (**c**) and dorsal (**d**) views. Bar = 4 cm.

plastral characters. However, some of its Wasatchian and Bridgerian 'species' have characters of the dorsal shell either plesiomorphic or homoplastic with those which are present in the early Eocene lineages referred to *Palaeochelys sensu lato*. This explains the hypothesis of relationships expressed by Hutchison (1988), and not accepted here. Because it appears to us certain that no North American genus is known in Europe in the Eocene, at least until now, the likely hypothesis is that this family, of Asiatic origin (Broin 1977, Hutchison 1998), radiated and dispersed in two directions, to North America via Beringia, and westward to Europe. This family is still very abundant in Asia, with some living Geoemydinae (*Mauremys*) being close to the ancient lineages present in Europe ('*Palaeochelys*' *sensu lato*).

Terrestrial Testudinidae evolved from one branch of the paraphyletic Geoemydinae, presumably in Asia. Terrestrial testudinines reached Europe and North America after the Paleocene-Eocene boundary interval, still in the early Eocene: *Hadrianus sensu stricto* in the late Wasatchian in North America (Hay 1908, Hutchison 1980), and '*Hadrianus*' *sensu lato* in the European Cuisian (MP10). It appears that the lineages are different on the two continents, having different shapes of the dorsal epiplastral lip (Fig. 3c,d). The explanation is that the subfamily reached and radiated independently in Europe and North America (Lapparent de Broin 2000, 2001, 2002). The Ellesmere testudinid confirms the northern route followed by the North American forms (Hutchison 1980).

The Carettochelyidae are known since the end of the Jurassic or early Cretaceous of China (Young & Chow 1953, Broin 1977, Meylan 1992), and in definitive early Cretaceous of Laos, through genera that are not differentiated at the subfamily level. In the late Cretaceous, *Kizylkumemys* is present in Uzbekistan (Nessov 1977). This genus is an Anosteirinae, the subfamily found later in the Eocene of China and North America (references in Broin 1977, 1987). The early

Eocene European genus *Allaeochelys* (Fig. 3 a,b) is a member of the Carettochelyinae, a subfamily definitely known in Asia in the Eocene Salt Range of India (contra Broin 1977, who classified *Hemichelys* differently), and in the late early- early middle Eocene of Pakistan (*Chorlakkichelys*, Broin 1987). For this family too, it is clear that Anosteirinae dispersed from China to North America on one side, whereas Carettochelyinae dispersed westward to Europe, leaving later traces of their presence in the Eocene of Indo-Pakistan.

The Podocnemididae, pleurodire turtles, came to Europe from Africa, where the family is diversified in the terminal early Cretaceous of Morocco. They cannot have come from Asia, where the infraorder is globally unknown (the exceptions being some Indian forms of ancient Gondwanian origin).

On the whole, turtles offer a very strong evidence of differentiation of different groups in Asia followed by dispersal in two different directions: some through Beringia giving rise to the North American groups, others dispersing westward and giving rise to European taxa which have no close affinities to the North American forms. They also show that some Euro-African exchanges took place at Paleocene-Eocene boundary times.

EURASIATIC SAMPLING AND CLIMATIC PROVINCIALISM INFERRED FROM MAMMALS

The Eurasian landmass is huge. During the late Paleocene-early Eocene period, the mammalian fossil record is limited to some geographical extremes. The European record is limited to western Europe, leaving the large east European (or Russian) domain unsampled. Even on the limited extent of western Europe, a marked north-south provincialism has been found, separating a southern (Iberian and southern French) domain from a northern Paris-Anglo-Belgian domain (Godinot 1996, Marandat 1997, Smith 2000). This provincialism, first quantitatively assessed by Marandat (1997), seems to be mainly of climatic origin, and it does not fit with the

reconstruction of a seaway between France and Spain, the Pyrenean Basin (Dercourt *et al.* 2000, map 17). Whereas this seaway is described as linking Atlantic and Tethyan domains, detailed studies show that the Carcassonne Strait was narrow, and the sea was terminating in the eastern part during the Thanetian, being replaced by a basin having a continental filling (Sztrakos *et al.* 1997). A continuous seaway may have existed only during some transgressive maxima, and only intermittently. It was not an effective barrier for mammals between Spain and France, because the provincialism mentioned above unites Iberian and southern French faunas in the same bioprovince.

In Asia, the mammalian fossil record during late Paleocene and early Eocene times is limited to China and the Mongolian Plateau. Here too, a marked provincialism exists with the Mongolian Plateau being possibly drier, in any case covered with more open environments than the eastern and more southern Chinese domain (Tong & Wang 1998, Meng & McKenna 1998). This leaves very large areas without a fossil record, including all southeast Asia (Indomalayan domain), all the area from Tibet to central Asia, and large pieces of the northern territories. If those northern areas were probably not very hospitable during the 'cool' Paleocene, such was not the case of the two other large areas, which probably played an important role in the early history of the orders under consideration. One could also speculate about the possible role of the Indian plate (Krause & Maas 1990), which was coming close to Asia at the end of the Paleocene, possibly playing a role in the Paleocene-Eocene boundary events (Beck *et al.* 1998). However, the group with the clearest inferred Paleocene Asiatic diversification, the perissodactyls, does not show any Indian endemic families, whereas the artiodactyls show such endemism, documented in later periods through only one family, the Raoellidae. This is more suggestive of a scenario of dispersal into India followed by local

evolution of these artiodactyls; however, a more complex history can be suspected.

The marked climatic provincialism documented in Western Europe and Eastern Asia suggests that similar conditions will be found in the other large domains, allowing for complex scenarios of differentiation/dispersal. The environment of a corridor may be a limiting factor to dispersal. Among the groups considered here, the presence of two families of primates suggests that this fauna was primarily a forest-adapted one. From the composition of the dispersing Wasatchian-Neustrian mammals, it was speculated that the North Atlantic corridor was probably humid and forested (Godinot 1982). A possible confirmation stems from the revision of the Phenacodontidae. Whereas *Phenacodus* dispersed from America to Europe, its two relatives *Ectocion* and *Copecion*, which were more cursorially adapted (Thewissen 1990), did not. One can think that the latter were adapted to more open environments. In this context, the apparent lack of dispersal of turtles between North America and Europe raises a question: was the corridor unsuitable, lacking a dense network of rivers and lakes, or was the dispersal limited by ecological competition, with similarly adapted groups being present on both sides?

Concerning the Asia-to-Europe dispersal, similar factors may well have played a role. In the late early Eocene, the Andarak fauna of Kirghyzstan, deposited in seashore sediments, lacks any arboreal mammals, reflecting open environments (Averianov & Godinot 1998). If this situation prevailed during the existence of the Siberian Sea and characterized the whole Turgai region, dispersal of forest-adapted mammals and fresh water turtles may have occurred only at special periods of forests and wet areas in that region. Perhaps this happened during the Paleocene-Eocene boundary events, at or close to the thermal maximum. Such a scenario (and many others) would explain the sudden dispersal in northern territories of a largely forest-adapted mammalian fauna, accompanied by turtles

and lizards (see below). Other more western and northern regions might also have acted as environmental filters.

CONCLUSION

The biogeographical origin of the three orders Primates, Artiodactyla, and Perissodactyla can be constrained by the phylogenetic analyses of higher taxa. For them, an origin in Asia appears very likely, in agreement with the model of Beard (1998). For the family Hyaenodontidae, an origin in Asia is possible, but one in Africa is equally possible. More fossils are needed to test these hypotheses. We note that the dispersal of the Podocnemididae from Africa to Europe testifies to the possibility of Euro-African exchanges at that time. In their essay on the intercontinental dispersal of Holarctic mammals at the period considered here, Beard & Dawson (1999) listed the mammalian taxa restricted to North America and Asia, and those restricted to North America and Europe. From the absence of higher taxa restricted to Europe and Asia, Beard & Dawson concluded that there had been no direct dispersal from Asia to Europe. However, even on their lists, it is striking that only three among the Wasatchian modern immigrants are present: one restricted to North America and Asia, the Isectolophidae (and this group may well have dispersed from Asia to North America through Beringia), and the two others, Notharctidae and Equoidea, are restricted to North America and Europe. However, Beard & Dawson agree that these must have had an Asiatic origin. Thus, if they have not yet been sampled in Asia, maybe they were not present in eastern Asia, but present in other Asiatic areas (Fig. 1). If Beringia was the unique corridor of dispersal, why aren't there more Wasatchian modern taxa shared only by Asia and North America? Admittedly, the fossil record of eastern Asia, in spite of remarkable recent improvements, is still sparse and could deliver much more. But the recent discoveries do not seem to fill that gap.

Contrary to analyses of the origins of orders, which were more or less remote in time, it should be possible to precisely ascertain dispersal scenarios of the genera that dispersed (or ideally of the species). Mammals are very mobile, and when dispersal is made easy by geography and climate, it can be rapid. The 22 genera common to Europe and western North America must have covered a distance of roughly 5-6000 km. Those who dispersed from China to western North America may have had to cross 7-9000 km. A number of genera made it, some of them in an America to Asia direction, as shown by new taxa found in the Wutu fauna (e.g. paromomyids, Tong & Wang 1998). If the Wasatchian newcomers had come from Asia through Beringia, one might predict strong similarities at the generic level between those faunas. However, as we have seen above, such is not the case until now. In particular, the absence of notharctids and *Diacodexis*, the small number of hyaenodontids, and the presence of different families of perissodactyls are puzzling and lead us to defend a different dispersal scenario involving more central or southern parts of Asia (Fig.4). A scenario of western dispersal, to Europe and from there to North America, is confirmed by the phylogenetic analyses which point to some primitive sister taxa of Euramerican mammalian immigrants being present in Europe, and by the recent proposition of an ante-carbon isotope excursion (presumably ante-Wasatchian) age for the Dormaal beds (even if this age were contradicted, the phylogenetic analysis and its dispersal implications would still hold).

A scenario of direct Asia to Europe dispersal is in fact strongly suggested by the herpetofaunas. Two lizard families, the Agamidae and the Gekkonidae, were thought by Estes (1983) to have reached Europe directly from Asia. Agamidae, which are present in the earliest Neustrian Dormaal fauna (MP7, Augé 1993, Augé & Smith 1997), must have dispersed during the Paleocene-Eocene bounda-

ry interval, and Gekkonidae, which are known slightly later (MP8-9), may have followed soon after, or at the same time without being yet sampled. Among other groups present in the European Neustrian MP7 level, the Necrosauridae are probably restricted to Europe and Asia (the family is not well defined; the North American species which were referred to the 'Necrosauridae' are different from the European forms, and the latter have a close relative in the late Cretaceous of Asia; Augé pers. comm. 2002). Within the Glyptosaurinae, the genus *Placosaurus* is common to Europe and Asia during the Eocene, whereas another genus, *Glyptosaurus*, is found in North America. From these last two examples, Augé (1993) concluded that a direct route existed between Europe and Asia, excluding North America, which must have functioned very briefly. We add that carettochelyine and geoemydine turtles clearly dispersed directly from Asia to

Europe. All these demonstrate considerable terrestrial reptile dispersal between Asia and Europe during the Paleocene-Eocene boundary interval, reinforcing our interpretation of the mammalian record.

The western Asia to Europe dispersal is rendered more likely by new studies of the Siberian Sea sediments, suggesting Turgai dispersal of terrestrial forms (Iakovleva *et al.* 2001). Further analyses of the Dormaal and Le Quesnoy faunas, a better understanding of the succession of faunas in the early Neustrian, as well as new discoveries in Asia, should help to confirm or to contradict our hypothesis. This scenario, as extended to the wave of earliest Wasatchian mammalian immigrants, does not diminish the prominent role of Beringia as a dispersal corridor between Asia and North America, which gave passage to several waves before and many after the one considered here (Krause & Maas 1990, Beard 1998, Hutchison 1998). In the

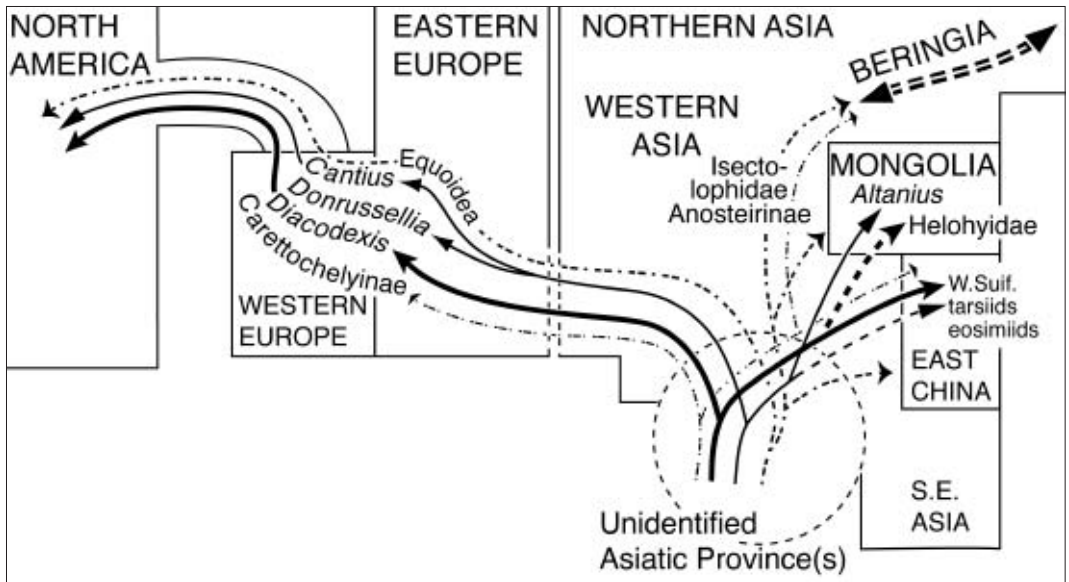


Figure 4 Paleogeographical sketch of continental areas showing a model of western and eastern dispersal in and out of Asia during the Paleocene-Eocene boundary interval from an unidentified region(s) of origin for some early primates (*Cantius*, *Donrussellia*, *Altanius*), artiodactyls (*Diacodexis*, W. Suif. = Wutu Suiform), two perissodactyl family groups (Isectolophidae, Equoidea), and for two subfamilies of carettochelyid turtles, Carettochelyinae and Anosteirinae. Tarsiids, eosimiids, and Helohyidae are known only later but conform to a similar pattern. This very simplified schema suggests that a complex Asiatic history and an Asia to Europe dispersal fit better the present fossil evidence than an all-Beringian dispersal. This dispersal would have involved also other genera, and it does not contradict earlier and later waves of dispersal through Beringia.

context of a direct Asia to Europe dispersal, other taxa common to, or closely related forms found on, both continents can be suspected. It could well be the case for cf. *Hyracolestes* (Marandat 1991). For the crocodile *Pristichampsus*, which arrived in the Cuisian and seems quite distinct from its North American counterpart *P. vorax*, we suspect a similar but slightly later scenario, exactly as the one we have inferred for terrestrial testudinines. More systematic work should enhance the evidence. Later arrivals in Europe (Cuisian) may indicate either stepwise dispersal through the Turgai region, or stepwise reaching of western Europe following one large Turgai dispersal. A better understanding of these events would be gained especially if a western Asiatic fossil record became available.

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