

Chapter 5

South American Mammals in the Paleocene of North America

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1. Introduction

Each of the major continents has given rise to a distinctive radiation of mammals at some point in its geological history. Faunal differences between continents generally reflect the chance composition of initial founding faunas, with subsequent endemic adaptation and coevolution constrained by the unique geological and environmental history of each continent. Faunal differences between continents also reflect, to some extent, fortuitous geographical relationships controlling opportunities for intercontinental faunal dispersal.

Continental positions have changed, sometimes markedly, in the past 100 million years, and climate and sea level too have changed. All three of these factors contribute to cycles of endemism and cosmopolitanism in the Cenozoic history of mammals. Here we are concerned with faunal relationships between two continents, North America and South America, whose geographical configuration has changed little in the past 65 million years. North America and South America have maintained a relatively stable north-south alignment through the entire Cenozoic (Smith and Briden, 1977), with connections between the two continents depending on a complex interaction involving changing sea levels and tectonic alteration of Caribbean and surrounding lithospheric plates.

North America and South America share a reasonably similar mammalian fauna in the latest Cretaceous (insofar as one can compare what little is known in South America with better-known Cretaceous faunas in North America). Marsupial mammals predominate in both, and placental mammals (eutherians) comprise a lesser component (Grambast et

al., 1967; Sigé, 1972; Clemens *et al.*, 1979; Marshall *et al.*, 1983a,b). Multituberculates, abundant in the late Cretaceous of North America, are unknown in South America. The presence of primitive marsupials and placentals on both continents is evidence of substantial faunal interchange, but so little is known of South American Cretaceous mammals (if indeed they are Cretaceous and not early Paleocene in age) that nothing can be stated with certainty about regions of origin or possible paths of dispersal.

The Paleocene and Eocene mammalian faunas of North America and South America are both reasonably well known, and they exhibit little evidence of faunal interchange. Indeed, the very high degree of endemism among mammals on both continents indicates that faunal interchange was very limited. My purpose here is not to review the early Cenozoic faunas of North America or South America in their entirety. This has been done most thoroughly by others, individually and collectively (e.g., Cifelli, 1983a,b; Ferrusquia-Villafranca, 1978; Marshall, 1982; Marshall *et al.*, 1981; Matthew, 1937; McKenna, 1981; Patterson and Pasqual, 1968; Paula Couto, 1978; Romer, 1966; Rose, 1981; Russell, 1967; Savage and Russell, 1983; Simpson, 1937, 1948, 1967, 1978, 1980; Sloan, 1969; Van Valen, 1978). Here I shall outline the limited evidence that exists favoring a late Paleocene faunal connection with minor dispersal from South America to North America. This minor dispersal event is part of an initial phase of the great Paleocene-Eocene faunal transition in mammalian evolution—a transition from faunas dominated by archaic Paleocene mammals to faunas dominated by Eocene representatives of the modern orders of mammals.

2. Mammalian Faunas of the North American Paleocene

The Paleocene mammalian faunas of North America are dominated by Multituberculata, primitive proteutherian insectivores, archaic ungulates of the order Condylarthra, and primitive plesiadapiform Primates (Sloan, 1969; Van Valen, 1978; Rose, 1981). Early and middle Paleocene representatives of the known orders of archaic placentals (principally Proteutheria and Condylarthra) are so primitive, generalized, and therefore similar, that it is sometimes difficult to tell them apart. Consequently, it is also difficult to recognize clear differences between the early and middle Paleocene faunas of North America (which are reasonably well known) and those of Europe, Asia, and Africa (which are as yet very poorly represented in the fossil record—early and middle Paleocene mammalian faunas are unknown in South America). Given this limited record, one is nevertheless impressed by the overall similarity of early and middle Paleocene faunas worldwide, suggesting a high degree of faunal cosmopolitanism, and continental interconnection, associated with the initial early Paleocene radiation of placental mammals.

The late Paleocene is a different story. By this time, some 5–10 million years after the initial Paleocene radiation of placentals, mammalian faunas of North America, Europe, Asia, and South America are all reasonably well known and some are highly distinctive, reflecting an important interval of faunal endemism. As noted above, multituberculates, proteutherians, plesiadapiform primates, and phenacodontid and arctocyonid condylarths predominate in North America. Many of the same families and even genera are known from the late Paleocene of Europe. However, Asian faunas are dominated by the orders Anagalida and/or Mixodontia (probably ancestors of rodents and lagomorphs), Pantodonta, and mesonychid Condylarthra. South American faunas are dominated by Marsupialia, didolodontid Condylarthra, and other primitive ungulates of the orders Litopterna and Notoungulata.

In contrast with faunas of the late Paleocene, early Eocene mammalian faunas of North America, Europe, and Asia share many of the same families and genera. Once the modern orders or modern representatives of Primates, Rodentia, Artiodactyla, Perissodactyla, and Carnivora appeared, in the latest Paleocene or early Eocene, they spread throughout the northern continents, reestablishing a broadly cosmopolitan holarctic mammalian fauna in

the early Eocene. Rapid dispersal of modern orders of mammals dominating holarctic faunas in the early Eocene had no apparent effect on South American mammalian faunas, indicating that South America was largely or entirely isolated during much of this important interval of faunal change.

The transition from endemic late Paleocene mammalian faunas to more cosmopolitan early Eocene mammalian faunas is now reasonably well known in North America, where it is best documented in the Clark's Fork Basin of Wyoming. Quantitative analysis of familial faunal composition across the Paleocene–Eocene boundary in the Clark's Fork and adjacent basins indicates that there was a reasonably smooth transition, at a familial scale of resolution, from faunas of the Tiffanian Land-Mammal Age (late Paleocene) to those of the Clarkforkian Land-Mammal Age (transitional Paleocene–Eocene), and a more rapid, although still reasonably smooth, transition from faunas of the Clarkforkian to those of the Wasatchian land-mammal Age (early Eocene). These transitions would appear more abrupt, obviously, at finer generic and specific scales of resolution. The pattern of change at a familial level can be illustrated diagrammatically using a multivariate principal components analysis and graphing component scores for each faunal sample against stratigraphic level ("prinstrat" plot in Fig. 1). In the diagram of Fig. 1, faunas of Tiffanian age plot in the center of the distribution of Principal Component I values and negatively (distally) in the distribution of Principal Component II values. Clarkforkian faunas plot at the right and proximally, while Wasatchian faunas plot at the left and proximally. There is, as shown, little overlap in the taxonomic balance of faunas representing each of the three land-mammal ages, and each, of course, occupies a distinct stratigraphic interval. Many families range through all three intervals, but differences between intervals can be recognized. Stated in terms of the families influencing the positions of faunas in a prinstrat plot, Tiffanian faunas are dominated by Plesiadapidae, Neoplagiaulacidae, Ptilodontidae, Carpolestidae, Arctocyoniidae, and Pantolestidae (in order of decreasing negative loadings on PC-II). Clarkforkian faunas are dominated by Phenacodontidae, Plesiadapidae, and Viverravidae (in order of decreasing positive loadings on PC-I), and Wasatchian faunas are dominated by Hyopsodontidae, Equidae, Adapidae, and Dichobunidae (in order of decreasing negative loadings on PC-I).

Interestingly, the four noninsectivore family groups making their first appearance in the North American fossil record during the Tiffanian (Arctostylopidae, Cyriacotheriidae, Epoicotheriidae/Metacheiromyidae, and Uintatheriidae) all have very small component loadings, indicating that they do not contribute greatly to the distinctiveness of Tiffanian faunas. Similarly, the four families that make their first appearance in the North American record during the Clarkforkian (Coryphodontidae, Esthonychidae, Ischyromyidae, and Miacidae) all have very small component loadings as well. Wasatchian Adapidae, Dichobunidae, and Equidae have large loadings, indicating that these new taxa contribute to the distinctiveness of Wasatchian faunas in a major way when they first appear. A comprehensive model explaining the evolution of mammalian faunas across the Paleocene–Eocene boundary is beyond the scope of this study. However, three of the four families or family groups making their first appearance in the Tiffanian belong to orders bearing close resemblance and likely affinity to South American mammals. These deserve careful consideration as they have a direct bearing on Paleocene faunal interchange between North America and South America.

3. South American Affinities of North American Paleocene Edentata, Notoungulata, and Dinocerata

The times of first appearance of North American Epoicotheriidae/Metacheiromyidae, Arctostylopidae, and Uintatheriidae are shown in Fig. 1. Each of these families appeared in North America during the late Tiffanian, and each bears some possible relationship to Paleocene mammals of South America.

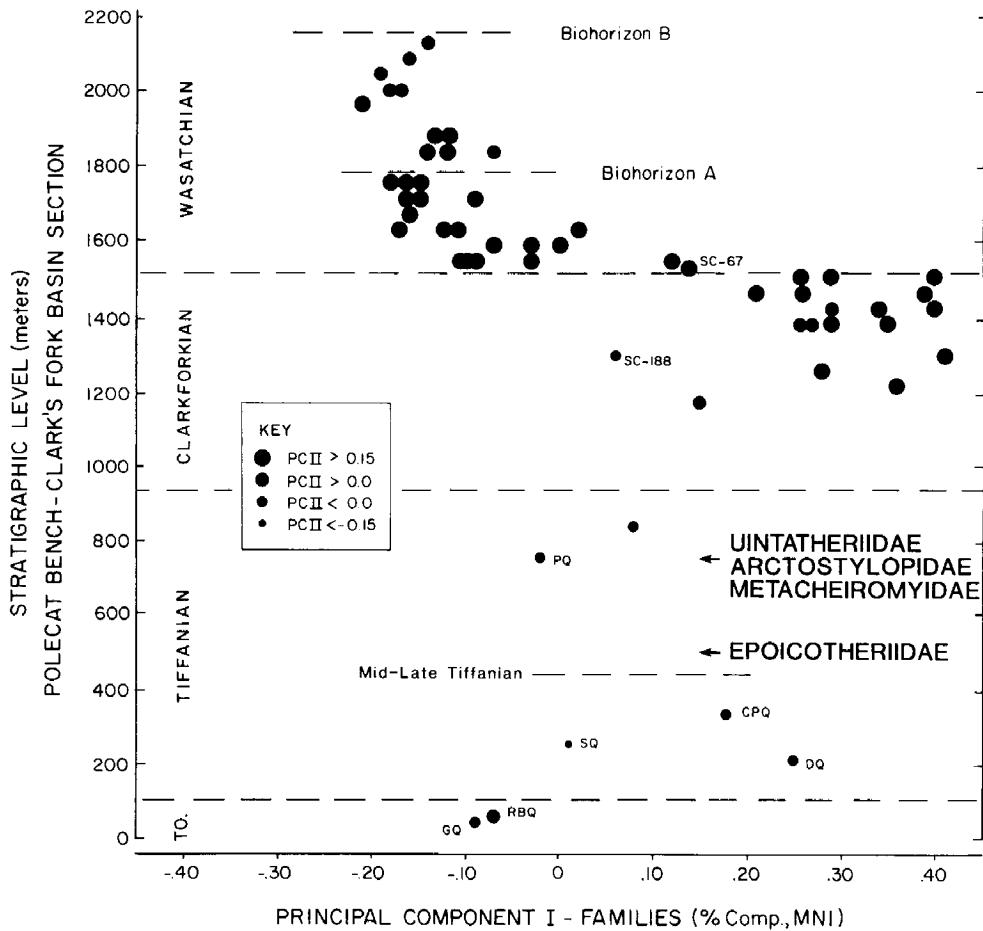


Figure 1. Multivariate principal components and stratigraphic (prinstrat) analysis of mammalian faunal composition comparing faunal samples of the North American Torrejonian, Tiffanian, Clarkforkian, and Wasatchian land-mammal ages in the Crazy Mountain Basin (Montana) and Clark's Fork and Bighorn Basins (Wyoming) of western North America. Abscissa is first principal component score (unscaled, including 54% of variance) based on percentage composition of minimum numbers of individual animals comprising each taxonomic family in each faunal sample (insectivores excluded). Minimum numbers of individuals for Paleocene quarry samples and SC-188 taken from Rose (1981); DQ from Krause and Gingerich, 1983); minimum numbers of individuals (MNI) for remaining surface samples estimated using total number of specimens (TNS) from each stratigraphic level and regression calculated from empirical data in Rose (1981), where $MNI = 1.02 TNS^{0.75}$. All quarry and surface samples analyzed here included a minimum of 30 specimens, and most are much larger. Total number of University of Michigan specimens from surface samples included in analysis is 8026. Ordinate is stratigraphic level above Cretaceous-Tertiary boundary, based on Polecat Bench-Clark's Fork Basin stratigraphic section in northwestern Wyoming. Second principal component score, including additional 18% of variance, is indicated diagrammatically by size of each solid circle (see key). Dashed lines represent episodes of significant coordinated faunal turnover. Overall pattern of faunal change illustrated here is one of a distorted helix, with general continuity but some indication of more abrupt shifts at land-mammal age boundaries. Allochthonous Epoicotheriidae appeared first, and Metacheiromyidae, Arctostylopidae, and Uintatheriidae appeared as a second group in the late Tiffanian, as shown. Each was rare and a minor component of late Tiffanian faunas, exhibiting little effect on overall faunal composition (see text). Locality abbreviations: CPQ, Cedar Point Quarry (Wyoming); DQ, Douglas Quarry, Montana; GQ, Gidley Quarry (Montana); PQ, Princeton Quarry (Wyoming); RBQ, Rock Bench Quarry (Wyoming); SC-67, basal Wasatchian on Polecat Bench (Wyoming); SC-188, Holly's Microsite and vicinity (Wyoming); SQ, Scarritt Quarry (Montana).

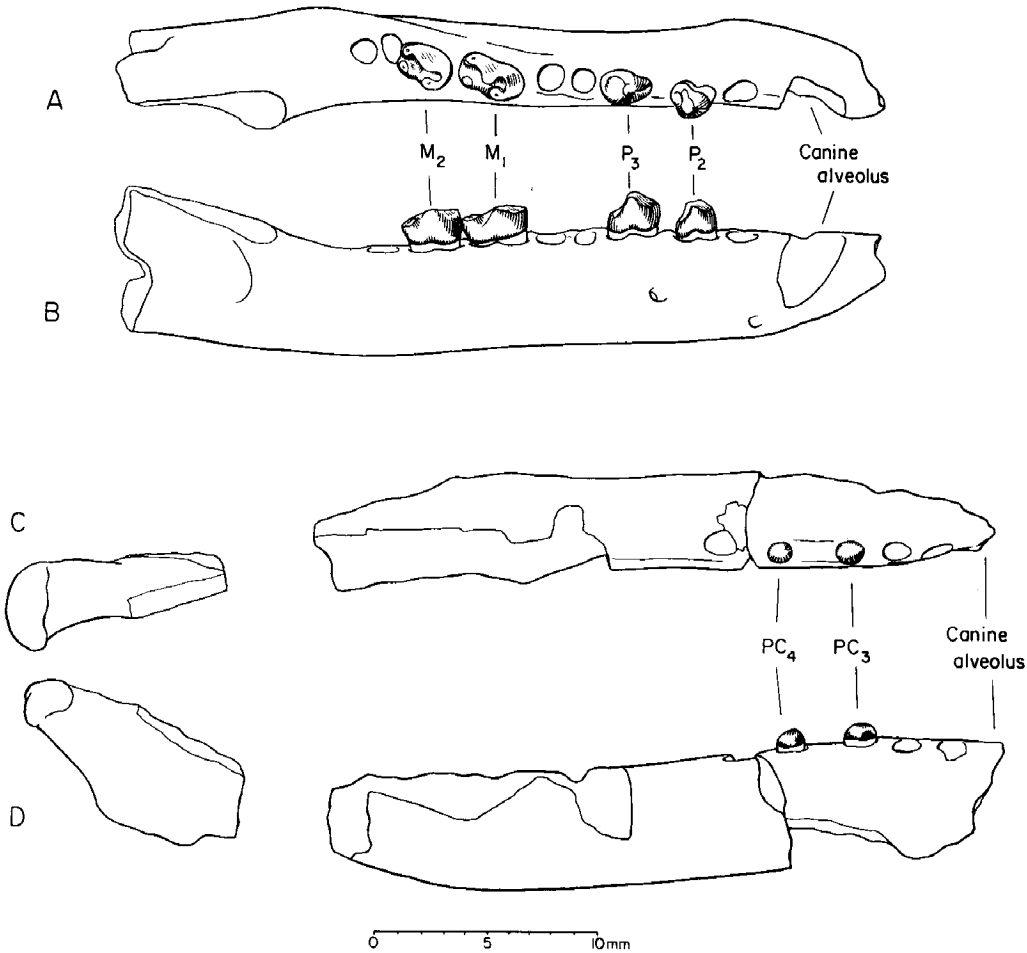


Figure 2. Comparison of the lower dentition of North American late Tiffanian Epoicotheriidae and Metacheiromyidae. (A) Occlusal and (B) lateral view of right dentary of epoicotheriid edentate *Amelotabes simpsoni* Rose 1978, Princeton University specimen no. 14855 (holotype), from late Tiffanian Witter Quarry in the northern Bighorn Basin, Wyoming. (C) Occlusal and (D) lateral view of right dentary of metacheiromyid edentate *Palaeonodon ignavus* Matthew 1918, University of Michigan [UM] specimen no. 66243 (reversed), from early Wasatchian locality SC-87 in the Clark's Fork Basin, Wyoming. Note full mammalian complement of seven cheek teeth, double-rooted cheek teeth, and retention of enamel on molars of *Amelotabes*. Note also reduced number of five peglike postcanine (PC) cheek teeth characteristic of Metacheiromyidae.

3.1. Edentata (Epoicotheriidae and Metacheiromyidae)

The oldest North American edentate, *Amelotabes simpsoni*, described by Rose (1978), is illustrated in Fig. 2. *Amelotabes* is regarded as the most primitive member of the family Epoicotheriidae, placed in the suborder Palaeanodonta. It is distinctive in retaining many primitive characteristics: having a shallow dentary with a large canine, retaining four pre-molars (P₂₋₄ are double-rooted), and having molars with low, poorly defined cusps and thin enamel. *Amelotabes* is closely related to another late Tiffanian genus, *Propalaeon-*

odon, the oldest metacheiromyid palaeodont, described by Rose (1979) from a locality near Princeton Quarry in the Clark's Fork Basin of Wyoming. *Propalaeonodon* is younger than *Amelotabes*, and it is plausibly derived from this genus. *Palaeonodon*, illustrated in Fig. 2 for comparison with *Amelotabes*, is a Clarkforkian and Wasatchian descendant of *Propalaeonodon*. Consideration of all known Palaeonodonta, epoicotheriids as well as metacheiromyids, indicates that they are most similar to *Xenarthra* (the group including living South American armadillos, sloths, and anteaters; see Simpson, 1931) and to *Pholidota* (Old world pangolins; see Emry, 1970). Palaeonodonts may be closely related to one or both of these modern orders (Rose, 1979).

Extension of the ranges of Epoicotheriidae and Metacheiromyidae back to the late Tiffanian (Rose, 1978, 1979) and recent discoveries of a European middle Eocene pholidotan, *Eomanis waldi*, resembling living pangolins (Storch, 1978), a possible European middle Eocene xenarthran, *Eurotamandua joresi*, resembling South American myrmecophagid anteaters (Storch, 1981), and a European Oligocene palaeonodont (Heissig, 1982), makes close relationship of palaeonodonts, pangolins, and xenarthrans more plausible geographically. Allocation of *Ernanodon*, from the "late Paleocene" of China (Ting, 1979; Radinsky and Ting, 1984), to such a broadly construed order Edentata is also plausible geographically (see below).

3.2. Notoungulata (Arctostylopidae)

The first specimen of a notoungulate to be found in North America was collected in 1913 by William Stein, a recent emigrant from Germany living in Otto, Wyoming, and employed for several summers by the American Museum of Natural History as a field collector. The specimen was found in sediments of Clarkforkian age at the head of Big Sand Coulee in the Clark's Fork Basin, Wyoming. This discovery, the first evidence of notoungulates outside South America, was initially greeted with skepticism, as such new records usually are. Two letters regarding the find are of historical interest and importance. The first, from W. D. Matthew of the American Museum to Stein in Wyoming, questions the authenticity of the find, and the second, Stein's reply, leaves little doubt in this regard.

December 2, 1913

My dear Stein

We have now unpacked and looked over the collection you sent in, and I am glad to be able to congratulate you on a very successful season. Considering the small size of your party and the short season you put in, you have secured a larger and better collection than we had expected. It is not so strong on *Coryphodon*, but it has a large series of the smaller things, and there are two finds of first class importance to science. One is a good lower jaw of the "*Bathyopsis*" out of the Clark's Fork beds, which turns out to be, as we had suspected it might, not *Bathyopsis* but a primitive ancestor. The other is a lower jaw of a very small animal which is related to the "Notoungulates" of South America, an extinct order never before found outside of that continent. This ranks with Granger's discovery of an armadillo [*Metacheiromys*, type genus of edentate Metacheiromyidae] in the Bridger, and will be a great surprise to the palaeontologists.

Now some of the palaeontologists will not be willing to believe in this find if they can help it, and they may suggest that you found the specimen when you were with Loomis in Patagonia and got it mixed in accidentally with your Wasatch collection. It is just possible that you might have picked it up in Patagonia, wrapped it in cotton and tucked it in some out of the way pocket of your coat, and then missed it when you came to turn in your finds at camp there. It might then stay in that pocket when you brought the coat back, and if you were wearing the same coat in the Big Horn Basin, you might find it when you came to turn out your finds at night, and not remembering it, have supposed you had found it in the Wasatch beds. Of course if you were not wearing the

same outfit, or if you remember finding the specimen it would disprove any such explanation.

The specimen in question is No. 79 of your list, marked "W.S." coll'r, "Head of Big Sand Coulee (upper beds), 9-4," and identified as "Rodent(?)". It was a lower jaw with two premolars and three molars on it, unworn, total length about $\frac{3}{4}$ inch, and was in three pieces. The jaw is chocolate brown, the teeth black. I enclose a rough sketch to help in identifying it.

If you can recall finding this specimen it will settle the matter. If you don't recall it, you may be able to state definitely that you were not wearing the same coat or to say whether there is any other possible way that a specimen found by you in Patagonia could have gotten mixed in with this collection. Will you write to me as soon as you can about this, as I want to exhibit the specimen at the Palaeontological Society meeting Christmas week. There are several other rare things in the collection, and some that may be entirely new. You must have put in a lot of hard work to get so much in the time out of those barren bad lands.

Sincerely yours,
W. D. MATTHEW
Curator
[American Museum of Natural History]

To which Stein replied (quoted verbatim):

December 8, 1913

Dear Dr. Matthew

Yours of the 2th come to hand today. I have been worried over the collection. I thought the quantity was to small, through my ignorance I did not know the quality of the fossils. Your kind letter was sure relieve to me, and I thank you for the congratulation. Yes we did work hard. We went in and over places wich was considerate impossible in summer time and drink water wich was thick with Wasatch clay!

In regard to the specimen no. 79 it was find by me as stated on label and in record book by Mr. Turner. I even remember the place. I find the two end pieces side by side but the mittle part was missing but after looking arond a few minute and utter some very strong word I was able to locate it a few feet below the others in a crack.

The specimen was new to me and we record it as "Rodent?" as we did with several others "rodent"like jaws wich we could not identify definitely.

You said that the palaeontologists may not be willing to believe in this find, but its simply impossible for any of Prof. Loomises Patagonia collection to get mixed up with our Wasatch material last summer. I did not wear the same outfit not even the same prospectin bag. The only clothing I wear last summer was shirt, pare of overalls, socks and shoes. All bought from local store two years after my return from south.

The little jaw in question is find from Clarksfork Basin pure and simple and not misplaced specimen from Patagonia by me.

I sincerely hope that the American Museum will later be able to drive more light on the subject wich will strengthen our claim.

With best wishes for your Society meeting.

I remain yours very respectfully
WILLIAM STEIN
Otto, Wyoming

Matthew (1915) described the specimen in question as a new genus and species, *Arctosylops steini* (Fig. 3), in honor of its collector. Any remaining question about the provenance of this specimen was removed ten years later when notoungulates were found and described from Mongolia (Matthew and Granger, 1925). Matthew and Granger described a new genus of Arctostylopidae, *Palaeostylops*, from Gashato, which they regarded as being older and probably ancestral to North American *Arctostylops*. This led them to postulate

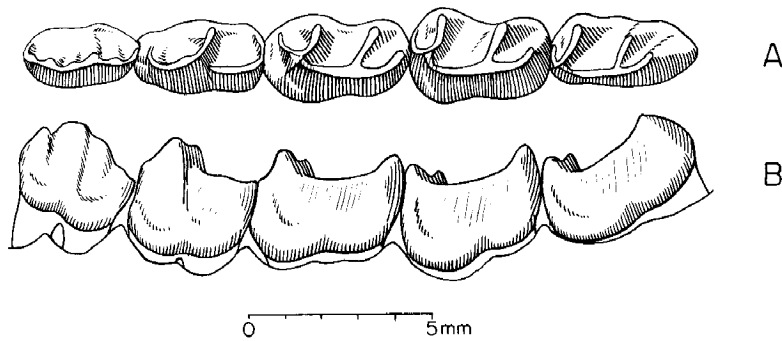


Figure 3. Lower dentition of *Arctostylops*, the only notoungulate known from North America and probably also the oldest notoungulate known outside South America. (A) Occlusal and (B) lateral view of left dentition of *Arctostylops steini* with P_{3-4} M_{1-3} , American Museum of Natural History no. 15922 (holotype), from Clarkforkian strata (early Eocene) at the head of Big Sand Coulee, Wyoming. Note distinctive anteroposteriorly oriented crest on lower molars shearing against a similar crest on opposing upper molars.

a northern derivation of South American notoungulates (Matthew and Granger, 1925, p. 2). A second North American specimen of *Arctostylops* was not recorded until 1969, when Jepsen and Woodburne (1969) noted discovery of a specimen from late Tiffanian sediments near Princeton Quarry in the Clark's Fork Basin. Intensive collecting in this area during the past ten years has yielded five more specimens, one from the Princeton Quarry level (late Tiffanian) and four from the Clarkforkian (Rose, 1981).

3.3. Dinocerata (Uintatheriidae)

The third group of interest here, Uintatheriidae (order Dinocerata), makes its first appearance in North America in the same narrow stratigraphic interval as the metacheiromyid *Propalaeonodon* and the notoungulate *Arctostylops*. The oldest well-dated records, all fragmentary, are from the vicinity of Princeton Quarry. Again one genus appears to be involved, *Probathyopsis* Simpson, and it is a rare component of late Tiffanian faunal samples (*Bathyopsoides* Patterson, a possible synonym of *Probathyopsis*, may also occur in sediments of latest Tiffanian age). The South American Paleocene genus *Carodnia* Simpson has been compared with *Probathyopsis* since it was first described. In describing *Carodnia*, initially based on an isolated left M_3 from the Riochican of Patagonia, Simpson (1935, p. 21) noted: "*Carodnia* resembles the primitive uintathere *Probathyopsis* more closely than any other animal known to me." Subsequently Paula Couto (1952, 1978) described more complete specimens of *Carodnia* from Itaborai in Brazil. Paula Couto (1952) compared *Carodnia* favorably with uintatheres, but placed it in a new mammalian order Xenugulata. Wheeler (1960) too compared *Carodnia* favorably with uintatheres. Dentally, *Carodnia* resembles *Probathyopsis* in having the same distinctive triangular P^{3-4} and M^3 , and very similar P_{3-4} and M_3 (Fig. 4). *Carodnia* differs from *Probathyopsis* in having a more reduced anterior dentition, enlarged pointed $P^{2/2}$, and much more lophodont M^{1-2} and M_{1-2} . These differences are probably sufficient to justify taxonomic ranking in its own family Carodniidae. However, by comparison with the morphological diversity within other known orders of early Cenozoic mammals, it is also reasonable to include *Carodnia* and Carodniidae with *Probathyopsis* and other uintatheriids in the order Dinocerata (McKenna, 1981).

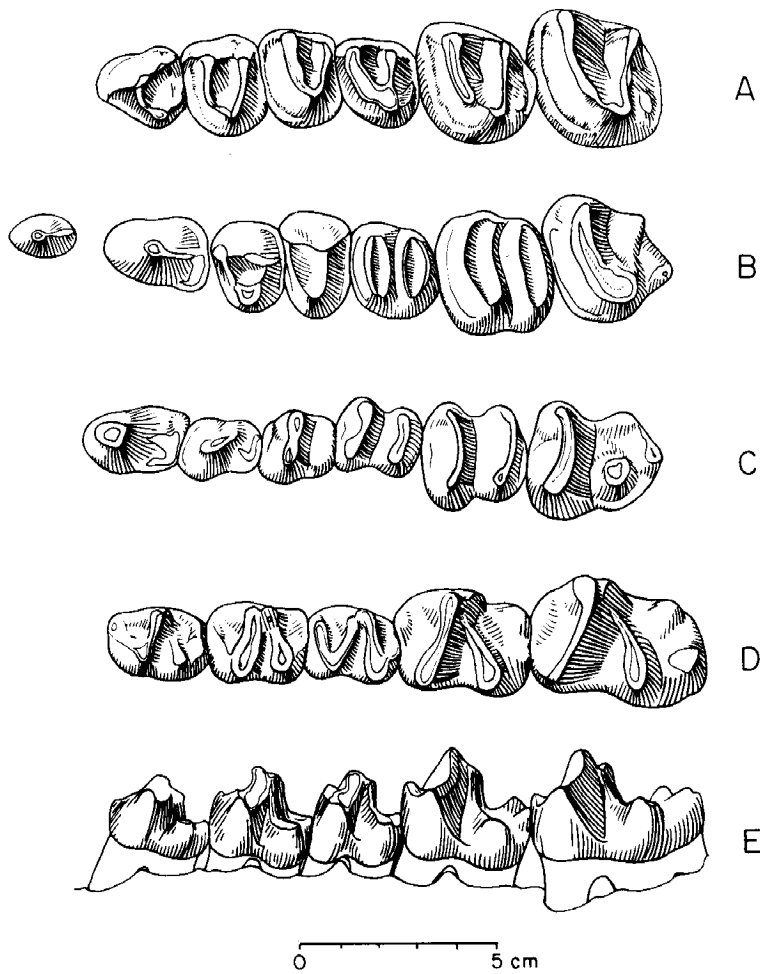


Figure 4. Comparison of the upper and lower dentitions of South American Paleocene *Carodnia vieirai* Paulo Couto from Itaborai in Brazil with those of North American early Eocene *Probathyopsis praecursor* Simpson from Clarkforkian strata (early Eocene) in the Hoback Basin, Wyoming. (A) Left maxillary dentition of *Probathyopsis* with P^3 – M^3 in occlusal view (UM 27250, reversed). (B) Left maxillary dentition of *Carodnia* with P^1 – M^3 in occlusal view (redrawn from Paula Couto, 1978, Fig. 1 and 2). (C) Left lower dentition of *Carodnia* with P_2 – M_3 in occlusal view (redrawn from Paula Couto, 1978, Fig. 1). (D and E) Left lower dentition of *Probathyopsis* with P_3 – M_3 in occlusal and lateral view (UM 27249). Note general similarity of all cheek teeth. *Carodnia* differs from *Probathyopsis* principally in having more pointed premolars and fully bilophodont first and second molars.

Cifelli (1983a) grouped *Carodnia* with South American pyrotheres because both were said to lack a cuboid facet on the astragalus. However, an erratum sheet distributed by the author with separates of this paper indicates that *Pyrotherium* has a well-developed cuboid facet on the astragalus, which, according to Cifelli, “considerably weakens my argument for a pyrotherian relationship for *Carodnia*.” The weight of published judgment certainly favors some relationship between *Carodnia* and untatheres.

4. Discussion: Paleocene Climates and Biogeography

None of the North American genera or families of mammals discussed here is known from South America. Taken individually, each genus or family might be considered weak evidence of a faunal connection between the two continents during the Paleocene. However, Epoicotheriidae/Metacheiromyidae, Arctostylopidae, and Uintatheriidae all made their initial appearances during the late Tiffanian land-mammal Age in North America. Coordinated appearances often indicate an allochthonous origin. The fact that Metacheiromyidae, Arctostylopidae, and Uintatheriidae appear together in the same restricted Princeton Quarry interval of the late Tiffanian suggests that these three families may well have shared a common center of origin. Considering their affinities with South American edentates, notoungulates, and xenungulates, this center or region of origin is likely to have been in equatorial South America. The pattern of changing worldwide climates during the late Paleocene lends further support to this idea.

4.1. Paleocene Climates

The history of climatic change during the Paleocene, at least at middle latitudes, begins with an early or middle Paleocene interval of warm temperatures and tropical or subtropical climate. The beginning of the late Paleocene was a time of climatic cooling, with temperate levels prevailing early in the late Paleocene. This temperate interval was followed by progressive warming, returning middle latitude climates to their former subtropical levels during the early Eocene (Wolfe and Hopkins, 1967; Buchardt, 1978; Wolfe, 1978; Hickey, 1980). Matching faunal diversity trends (Rose, 1981) to this general pattern suggests that the Torrejonian Land-Mammal Age was probably subtropical, followed by a temperate or warm temperate early and middle Tiffanian land-mammal age, with progressive warming during the late Tiffanian and much of the Clarkforkian and Wasatchian.

Worldwide climatic cooling would have the effect of constricting geographic ranges, moving all limits toward the equator. Warming climates, on the other hand, would have the opposite effect, expanding the limits of geographic ranges away from the equator. The general direction of faunal movement during times of climatic cooling should be equatorward, whereas the direction of faunal movement during times of climatic warming should be poleward. Thus it is most reasonable to interpret the appearance of allochthonous Epoicotheriidae and Metacheiromyidae, Arctostylopidae, and Uintatheriidae in North America during the late Tiffanian, a time of climatic warming, in terms of northward dispersal from a more southerly center of origin. Given the taxonomic affinities of these families with other South American groups, the coordinated appearance of all of them in North America during the late Tiffanian seems to indicate at least limited faunal exchange between South America and North America. Judging by the advanced evolutionary grade of all three families, this faunal exchange probably took place early in the late Paleocene, during the early or middle Tiffanian land-mammal Age.

If *Perutherium altiplanense* is a notoungulate, as Marshall *et al.* (1983a) have proposed, its presence in South America in the latest Cretaceous (or early Paleocene) predates the appearance of notoungulates in North America and Asia. Thus the chronological and geographical distribution of notoungulates is consistent with an equatorial South America-to-North America (-to- Asia) pattern of dispersal of notoungulates.

4.2. Paleocene Biogeography

In order to understand the Paleocene biogeographic history of North America, it is important to consider the configuration of surrounding continents and potential connections between them. During Paleocene time, North America and South America occupied

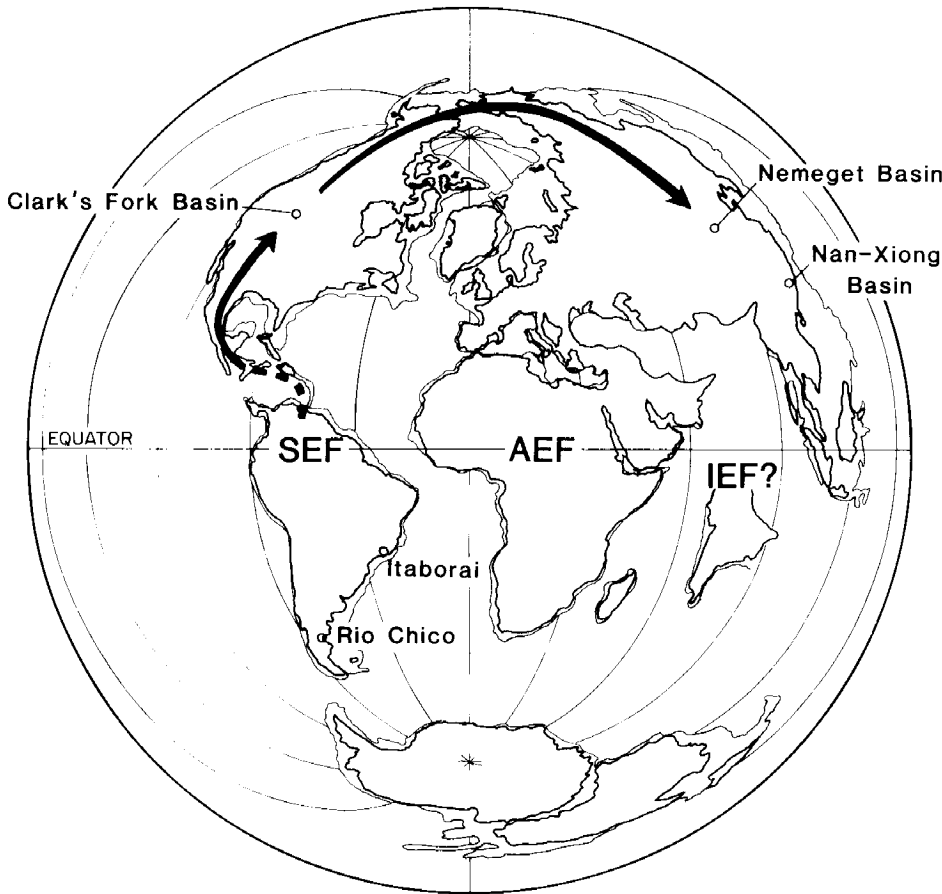


Figure 5. Reconstructed geographic relationships of the major continents during Paleocene time. Note that North America and South America were in approximately their present position relative to each other. Note also that an equatorial tropical climatic belt crossed northern South America during the Paleocene, very much as it does today. This tropical climatic belt probably acted as a filter complementing a tectonically unstable Caribbean region in separating subtropical and temperate South American faunas from those of subtropical and temperate North America. Asymmetry of geographic and faunal barriers might account for the greater success of equatorial South American mammals dispersing to North America and the apparent failure of North American mammals to invade South America. Principal Paleocene or earliest Eocene mammalian localities in South America are near Rio Chico (Argentina) and Itaborai (Brazil); in North America are in the Clark's Fork Basin (Wyoming, U.S.A.); and in Asia are in Nemeget Basin (Mongolia) and Nan-Xiong Basin (China). SEF represents the South American equatorial fauna, a likely source for South American Paleocene mammals invading North America and a second barrier for North American mammals crossing the Caribbean. AEF and IEF? represent postulated African and Indian equatorial faunas. Heavy lines show proposed path of dispersal of edentates(?), notoungulates, and uintatheres from South America to North America, and finally to eastern Asia. Lambert equal-area projection based on map 44 in Smith and Briden (1977).

approximately their present configuration (Fig. 5), with a potential connection in the Caribbean region (see Donnelly, Chapter 4, this volume; Gose, Chapter 11, this volume). Similarly, North America and Asia occupied approximately their present configuration, being connected at high latitude via the Bering area. North America and Europe were more closely connected during the Paleocene than at any later time, again at high latitude, because the

northern Atlantic Ocean had not yet rifted to its present breadth (see McKenna, 1983, for review). It is reasonable to assume that mixing of faunas across equatorial barriers is not a function of worldwide temperature since equatorial regions are least affected by change in such climatic parameters. However, intercontinental connections at high latitude are clearly much more sensitive to climate, since it is only during warm intervals that tropical and subtropical continental faunas would find such routes inhabitable.

Evidence seems to favor introduction of a limited number of South American mammals into North America during the late Paleocene. However, the highly endemic nature of South American Paleocene faunas gives no evidence that such a late Paleocene event involved dispersal of North American taxa to South America. This one-way dispersal of Paleocene mammals may be related to one-way tectonic movement of microplates or continental fragments carrying mammals from South America to North America, with continental fragments functioning as "Noah's Arks" (McKenna, 1973). However, current emphasis on vertical tectonics in the Caribbean (Donnelly, Chapter 4, this volume) lends little support to this idea. It is perhaps more likely that the broad equatorial climatic/floral/faunal zone spanning northern South America (SEF in Fig. 5) acted as a second filter, functioning in combination with ephemeral land bridges across the Caribbean to inhibit significant penetration of North American emigrants into South America. It is important to recognize that all known Paleocene mammalian faunas in South America (principally those near Itaborai and Rio Chico) are well south of this South American equatorial zone. The filtering effect of a broad equatorial biogeographic province like that spanning northern South America during the Paleocene should not be underestimated. It would undoubtedly have had a strong inhibiting effect on any continental faunal emigrants from North America attempting to penetrate the central and southern parts of South America where all Paleocene fossil localities are located.

Any South American taxon likely to invade North America by crossing the Caribbean seaway would necessarily already inhabit the northern margin of the South American equatorial zone, and northward dispersal would not involve crossing a second barrier of the magnitude of an equatorial climatic/floral/faunal zone. Late Tiffanian climatic warming would facilitate the early appearance of new immigrants coming to North America from South America by minimizing the climatic gradient they faced in reaching middle latitudes of Wyoming where many of the most productive fossil-bearing strata known in North America are located.

Edentata, Notoungulata, and Dinocerata are not, by nature, particularly good dispersers and colonizers, suggesting that the late Paleocene crossing from South America to North America required a land bridge of some kind or a chain of closely spaced islands. It is interesting to note in this regard that rodents and primates of modern aspect invaded North America from Europe and/or Asia in the Clarkforkian and Wasatchian, just after the appearance of edentates, notoungulates, and dinoceratans. Rodents and primates of modern aspect are generally regarded as excellent colonizing species, and yet they were evidently unable to colonize South America until the Oligocene. Failure of rodents and primates to colonize South America in the early Eocene suggests that the late Paleocene land bridge or chain of islands was short-lived, disappearing before rodents and primates were able to take advantage of it.

Climatic warming evidently continued after Edentata, Notoungulata, and Dinocerata first appeared in North America, and representatives of each of these orders are known in the latest Paleocene or earliest Eocene of Asia. If the biogeographic hypothesis outlined here is correct, then each of these groups becomes important for correlating Asian mammalian faunas with those of North America. The earliest edentate (*Ernanodon*), notoungulates (*Sinostylops*, etc.), and dinoceratans (*Prodinoceras*, etc.) in China are in faunas broadly correlated as "Archaeolambda faunas" to distinguish them from earlier "Bemalambda faunas" (each named for the endemic Asian pantodont most commonly associated

with them; see Li and Ting, 1983, for review). In Mongolia, the earliest notoungulate (*Palaeostylops*) and dinoceratan (*Prodinoceras*) occur together in the uppermost Zhigden and lower Naran members of the Naran-Bulak Formation (Dashzeveg, 1982). Allowing a brief interval of latest Tiffanian time for edentates, notoungulates, and dinoceratans to reach Asia from North America, the *Archaeolambda* or notoungulate-dinoceratan faunas of China and Mongolia are not likely to be older than early Clarkforkian (very latest Paleocene) on a North American time scale.

5. Summary

Three groups of mammals appearing in the late Tiffanian (late Paleocene) of North America bear close resemblance to distinctive, highly specialized mammals known from the Paleocene of South America. Each of these groups, edentate Epoicotheriidae/Metacheiromyidae, notoungulate Arctostylopidae, and dinoceratan Uintatheriidae, might constitute weak evidence of faunal dispersal from South America, but taken together they provide substantial evidence for such a late Paleocene dispersal event. Geographic and tectonic factors favoring such a dispersal must have been short-lived, because North American early Eocene rodents and primates, appearing shortly after the edentate-notoungulate-dinoceratan dispersal event, were unable to invade South America. Climatic warming during the late Tiffanian is consistent with dispersal of edentates, notoungulates, and dinoceratans northward from equatorial South America, and representatives of all three of these groups have been described from "late Paleocene" *Archaeolambda* faunas in China and Mongolia (these *Archaeolambda* faunas are here regarded as post-Tiffanian, i.e., Clarkforkian, in age).

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