
Land Mammals and the Great American Interchange
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Land Mammals and the Great American Interchange

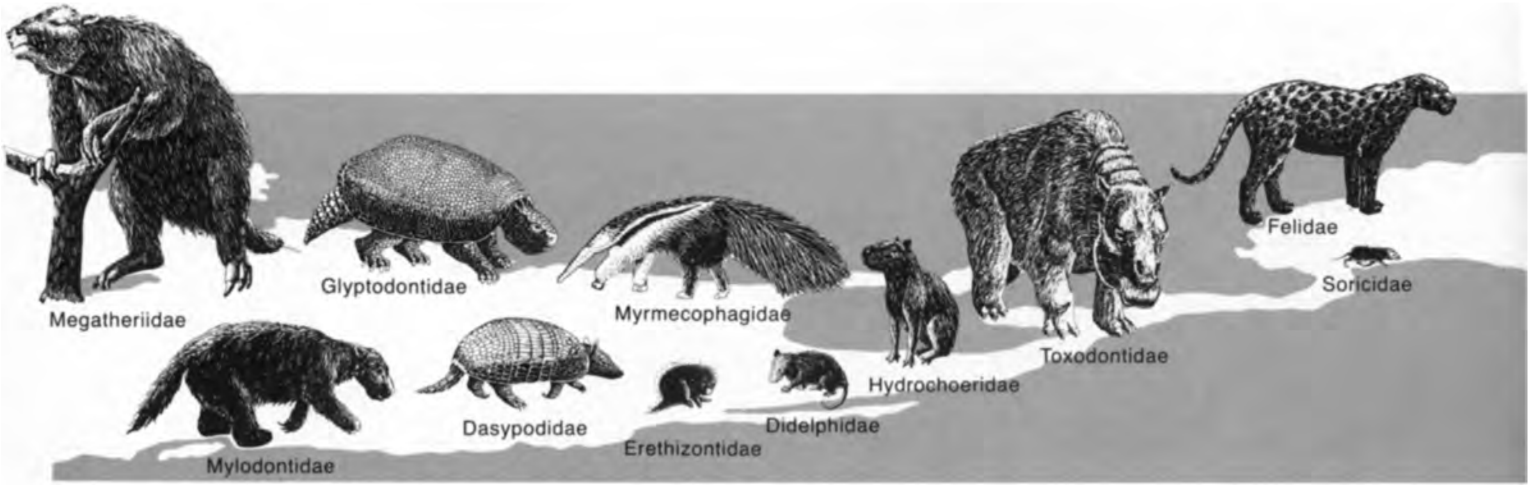
Larry G. Marshall

The continents of South America, Africa, Antarctica, Australia, and India were once joined in a large land mass in the southern hemisphere called Gondwana. About 100 million years ago (MYA) South America began to separate from Africa, moving in a primarily westward direction. There is no convincing geological evidence to indicate that South America had a continuous land connection with any other continent until about 3 MYA, when the Bolivar Trough marine barrier disappeared and the Americas were united by the emergence of the Panamanian land bridge. The long-isolated continental biotas of North and South America were brought into contact, resulting in an intermingling that has come to be known as the Great American Interchange (Webb 1976; Fig. 1). The site of the former Bolivar Trough is thus the gateway for this event, denoting the historical boundary between two biotic provinces (Fig. 2). Although many different groups of plants and animals took part in the interchange, I will focus on land mammals, which are the most thoroughly studied of the participants.

The emergence of the Panamanian land bridge three million years ago permitted the mingling of the long-separated faunas of North and South America

The Great American Interchange was first recognized by Wallace (1876), but it has taken another hundred years of intense paleontological study by Ameghino, Matthew, Scott, Patterson, Simpson, Webb, and others to clarify patterns of dispersal (see, for example, Marshall 1981, 1985; Webb 1985; Webb and Marshall 1982). It is only during the last decade, moreover, that greater precision in dating the sediments containing interchange taxa has provided a firm time frame for various aspects of the event. It is now possible to assess the interchange in detail, and to analyze the tempo and mode of dispersal and the rates of extinction and origination in successive faunas through time. As a result, the Great American Interchange represents the best-documented example in the fossil record of the intermingling of two long-separated continental faunas.

By the time of the interchange, the land mammal faunas of North and South America had distinct histories that shaped their character and taxonomic composition. During the Cenozoic (from about 66 MYA to the present), North America was connected at one time with Europe and on multiple occasions with Asia via Beringia, resulting in recurrent additions of Old World taxa (McKenna 1975; Repenning 1980; Russell and Zhai 1987). When the Great American Interchange began, the North American land mammal fauna was part of the vast Holarctic realm, and many families and genera occurred simultaneously in North America, Asia, Europe, and Africa. The taxa present in North America at the start of the interchange were thus the survivors of many earlier exchanges, tested repeatedly by immigrations and attempted immigrations from the Old World.



By contrast, during most of Cenozoic time South America was an island continent, like Australia today. As a result of this isolation, South American land mammals evolved in a world of their own; genera, families, and most orders were autochthonous and endemic to the continent, being found there and nowhere else. When the Great American Interchange began, the land mammals of South America were thus brought into contact with a major influx of potential competitors and predators for the first time in their history. In addition, South American taxa that dispersed to North America were first-time immigrants, entering a fauna that had known numerous earlier invasions. These differences in the histories of the North and South American faunas signal the fact that aspects of the interchange will be different on each continent.

South American land mammals

A brief look at the history of South American land mammals permits the identification of some direct consequences of the interchange, as opposed to changes that were inevitable or related to trends begun earlier. The constraints imposed on patterns of dispersal by South America's status as an island continent allow us to distinguish three main strata of land mammals (Simpson 1980; Fig. 3).

Stratum 1 consists of groups present in South America at or just before the beginning of the Cenozoic. Included are Marsupialia, Proteutheria, Pantodonta, Condylarthra, and Notoungulata, which are first recorded in rocks of late Cretaceous age, and Xenarthra, Xenungulata, Astrapotheria, Pyrotheria, and Litopterna, which are first found in rocks of middle and late Paleocene age in Argentina and Brazil (Marshall and de Muizon 1988; Marshall 1985). There is much debate as to whether some or all of these groups evolved in South America from long-established Mesozoic stock or whether they arrived there from elsewhere—Africa, North America, or Australia via Antarctica—just before or simultaneous with their first appearance on that continent. The important point here is that the stratum 1 groups were the first to radiate to fill land mammal niches and adaptive zones in South America in early Cenozoic time.

Stratum 2 groups include caviomorph rodents—for example, capybaras and porcupines—and monkeys, both of which are first recorded in rocks of middle Oligocene to early Miocene age. The oldest caviomorph rodents are known from a level dated about 34 MYA in Argentina; monkeys first appear about 26 MYA in Bolivia (Marshall 1985; MacFadden et al. 1985). These groups arrived either from Africa or (more probably) from North America sometime during the late Eocene time or earlier, traveling by the process of waif dispersal across the water barrier which then isolated South America from the other continents (Patterson and Wood 1982). Waif dispersal is thought to occur during times of flooding and high water levels, when rafts of vegetation may break away from the banks of swollen rivers and be carried to sea. Some of these rafts, it is speculated, may contain animals that can subsist on the materials provided by the raft itself. These miniature "Noah's arks" (McKenna 1973) may be carried by prevailing winds and currents to distant shores; upon successful docking, the voyagers disembark to colonize new lands. A prerequisite for successful waif dispersal is the survival of a pregnant female, a female with young, or a male-female pair able to perpetuate the species in a new land. The chances of a successful crossing are clearly low, and

Figure 1. The appearance of the Panamanian land bridge set in motion the event now known as the Great American Interchange, which resulted in a major restructuring of the widely differing biotas of North and South America. The land mammals shown on the isthmus and at the left are representative of the 38 South American genera that walked north across the land bridge; at the right are representatives of 47 dispersants from North America that arrived in South America by way of the land bridge. Unlike South American taxa, which showed little diversification after their immigration, North American land mammals experienced an explosive diversification following their arrival on the South American continent.

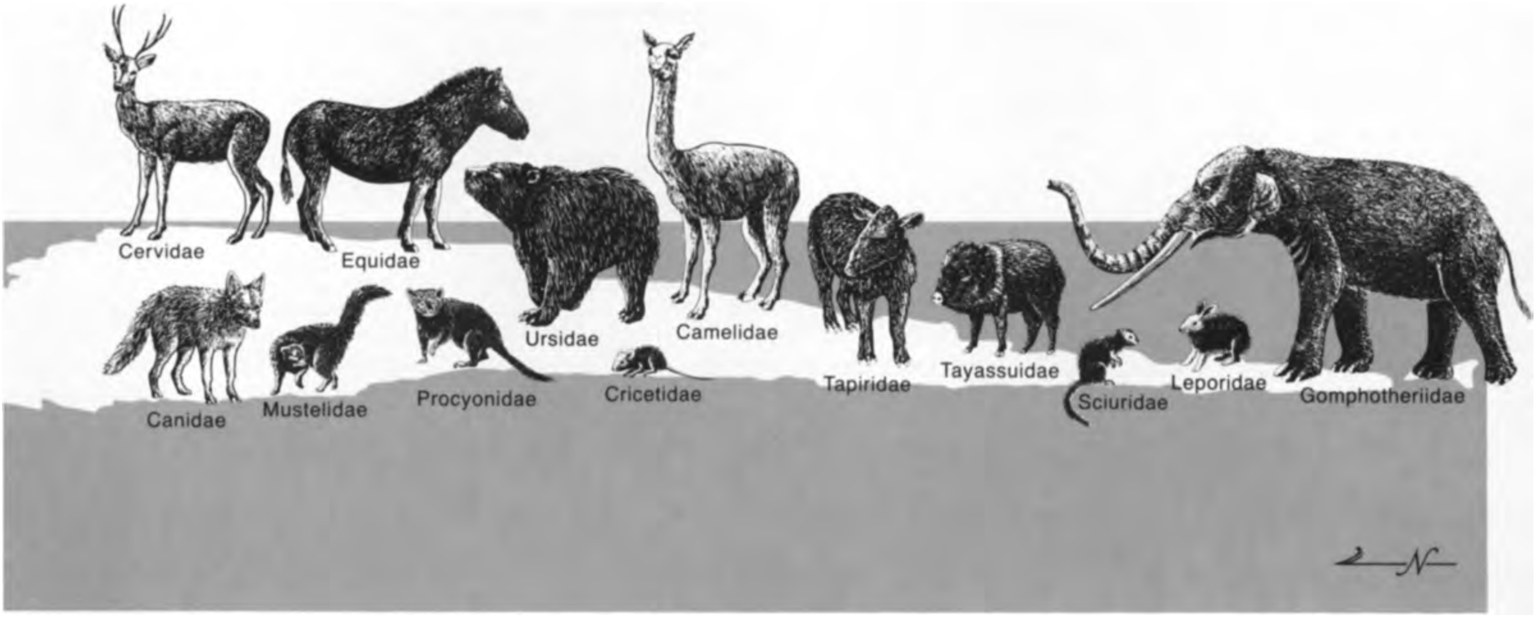


Figure 2. The Panamanian land bridge was formed by the uplift of the earth's crust in the region of the Bolivar Trough marine barrier (*colored area*), which once connected the Caribbean Sea and the Pacific Ocean across what is now southern Panama and northwestern Colombia. Colored dots indicate sites at which interchange fossils of late Miocene to early Pleistocene age have been found in Argentina, the southern and southwestern United States, and Mexico. Virtually nothing is known about the early part of the interchange in Central America and northern South America.

many voyagers that survived were no doubt unsuccessful in establishing a foothold. Nevertheless, many such Noah's arks probably existed, and some containing rodents and monkeys managed to reach South America.

Stratum 3 includes participants in the Great American Interchange. Two groups are recognized, based on the time and mode of dispersal: taxa that were waif dispersants in the late Miocene, before the emergence of the Panamanian land bridge, and taxa that walked across the land bridge after its final emergence about 3 MYA.

Waifs and walkers

During late Miocene time, a limited interchange of land mammals occurred between the Americas either by rafting across the Bolivar Trough or by island-hopping through the Antilles archipeligoes. South American immigrants of the ground sloth families Megalonychidae (*Pliometanastes*) and Mylodontidae (*Thinobadistes*) are first recorded in North America in rocks of early Hemphillian age, i.e., by 8 MYA (for North and South American ages, see Fig. 5). *Pliometanastes*, which was the size of a modern black bear, makes its first appearance in local faunas of this age in central Florida, New Mexico, and central California. This family gave rise to *Megalonyx*, a larger and more specialized ground sloth that occurs in rocks of late Hemphillian to Rancholabrean age. *Thinobadistes* is first known from the early Hemphillian of Florida and occurs with *Pliometanastes* in faunas of middle Hemphillian age in Florida and Texas (Webb 1985).

North American immigrants of the raccoon family Procyonidae are first found in South America in Argentinian rocks of Huayquerian age dating from about 7.5 MYA (Butler et al. 1984). The earliest procyonid genus, *Cyonasua*, was about the size of a large modern raccoon; by Ensenadan time this genus gave rise to the slightly larger *Brachynasua*, and later to the bear-size *Chapalmalania* (Marshall 1985).

Miniature "Noah's arks" may be carried by prevailing winds and currents to distant shores

These late Miocene waif dispersants had little impact on the overall diversity of the faunas they joined. However, they did become firmly established and themselves show a low level of diversification. The members of all three families appear to have been adapted to a wide range of habitats; *Thinobadistes* and *Pliometanastes* were large generalized herbivores, whereas *Cyonasua* was a large omnivorous carnivore (Webb 1985). This adaptiveness would have been advantageous on rafts, where food was limited, because these voyagers could have eaten virtually everything available to them. Judging from living relatives, *Cyonasua* may also have had swimming abilities that would have been useful had the raft sunk before docking.

The second group of immigrants was created by the emergence of the Panamanian land bridge, which resulted from a combination of tectonic changes and decreases in the sea level related to ice-cap formation, the separate effects of which are difficult to isolate (Cronin 1981; Savin and Douglas 1985). The first record of South American animals that walked north across the newly emerged land bridge occurs in rocks of late Blancan age that date from about 2.5 MYA. Seven genera of land mammals and one large ground bird appear almost simultaneously in faunas of this age in Florida, Texas, New Mexico, Arizona, and California. These immigrants consisted of two armadillos (*Dasypus* and *Kraglievichia*), a giant armadillo-like glyptodont (*Glyptotherium*), two ground sloths (*Glossotherium* and *Nothrotheriops*), a porcupine (*Erethizon*), a large capybara (*Neochoerus*), and a phororhacoid ground bird (*Titanis*).

The most interesting of these early dispersants is *Titanis*, which is believed to have reached a height of over 3 m (Brodkorb 1963; Fig. 4). Phororhacoids were flightless, carnivorous ground birds that showed marked running specializations in middle and late Tertiary faunas in South America (Patterson and Kraglievich 1960; Marshall 1978). They were the only large terrestrial carnivores on that continent when the land bridge appeared, and *Titanis* was the only large South American carnivore to disperse to North America, where it is recorded in faunas of late Blancan and early Irvingtonian age in Florida (Marshall 1977; Webb 1985). Phororhacoids have one distant living relative in Paraquay, *Cariama*, a long-legged, long-necked bird about 0.7 m tall, capable of running at a speed of 25 miles an hour; it resorts to spurts of short-distance flight only when necessary.

A second major contingent of South American taxa that crossed the land bridge appears in rocks of early Irvingtonian age dating from about 1.9 MYA in northwestern Mexico and numerous localities across the southern United States. These taxa include a giant armadillo (*Holmesina* = *Pampatherium*), a ground sloth (*Eremotherium* = *Megatherium*), a giant anteater (*Myrmecophaga*), and a capybara (*Hydrochoerus*). An opposum (*Didelphis*) appears in the late Irvingtonian of Florida, another ground sloth (*Meizonyx*) in the Irvingtonian of El Salvador, and a rhino-like toxodont (*Mixotoxodon*) in the Rancholabrean of southern Central America.

Of these genera, the rhino-like *Mixotoxodon* and the ground sloth *Meizonyx* are known only from southern Central America, and the anteater *Myrmecophaga* only from a single site in northwestern Mexico (Webb and Perrigo 1984; Shaw and McDonald 1987). Records of the latter two have been established only within the last four years, demonstrating that some aspects of the North American part of the interchange are still poorly documented. We now know many of the South American dispersants that reached the southern part of the United States but little of what happened along the way. *Mixotoxodon*, *Meizonyx*, and *Myrmecophaga* did not go to the end of the highway north, and further research in Central America will no doubt reveal that other dispersants also failed to do so. The number of dispersants should decrease as one goes from Panama to the United States, but due to the vagaries of the fossil record and a lack of knowledge of what happened in Central America, the reverse is now true.

The first unequivocal record of the presence of North American land mammals that walked south across the land bridge occurs in Argentinian rocks of Chapadmalalan age, dating from 2.8 to 2.5 MYA. Two taxa are represented: a skunk (*Conepatus*) and a peccary (*Platygonus*). A horse (*Hippidion*) appears at about the same time in faunas of early Uquian age (2.5 MYA) in northwestern Argentina.

Evidence of the main contingent of North American dispersants begins to appear in rocks of late Uquian age (2 MYA) in Argentina. Sixteen genera representing nine families have been found: dogs (*Dusicyon*, *Protocyon*), cats and saber-tooths (*Felis*, *Smilodon*), skunks (*Galictis*, *Stipanicicia*), bears (*Arctodus*), elephant-like gomphotheres (*Cuvieronius*), horses (*Onohippidium*), tapirs (*Tapirus*), camels (*Hemiauchenia*, *Lama*, and *Palaeolama*), and deer (*Blastocerus*, *Morenelaphus*, and *Ozotoceros*). Rabbits (*Sylvilagus*) and squirrels (*Sciurus*) appear in the Lujanian; shrews (*Cryptotis*), pocket gophers (*Orthogeomys*), and kangaroo rats (*Heteromys*) are known only in living faunas.

Field mice, found in North America as early as 9 MYA, first appear in South America in Argentinian faunas of late Montehermosan age, dating from 3 to 2.8 MYA. Two genera of these cricetids are represented there (*Auliscomys* and *Bolomys*), and four additional genera (*Akodon*, *Dankomys*, *Graomys*, and *Reithrodon*) appear in Chapadmalalan faunas (Reig 1978). There are now about 54 living genera of cricetids in South America. This group is not discussed above with the waifs or the walking dispersants because there is a great deal of debate about when and how it arrived in South America. Webb (1985) has admirably summarized two possible scenarios. The first attempts to account for the remarkable present-day diversity of cricetids by hypothesizing that they arrived as waif dispersants earlier than the first documented appearance in Montehermosan time (Hershkovitz 1966; Reig 1978). Reig observes that known fossils strongly suggest a much earlier arrival, probably at the beginning of the Miocene, with the main episodes of development taking place in the northern and central Andes, where fossil deposits are still poorly known. A slightly modified version of this theory holds that cricetids arrived during the period of world-wide low sea levels in the late Miocene, when the Bolivar Trough marine barrier was narrower and conditions for dispersal were optimal (Marshall 1979).

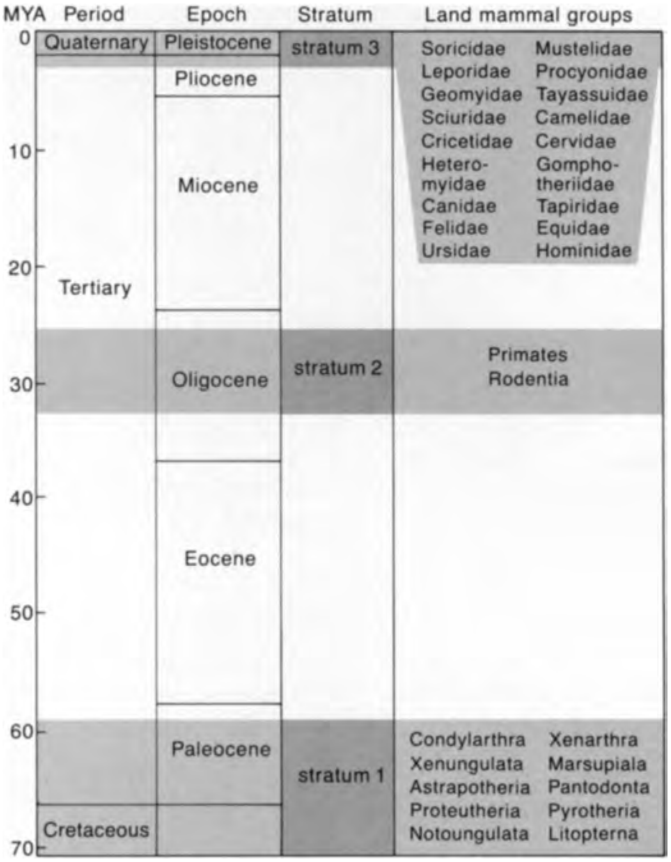


Figure 3. The fact that South America was once an isolated island continent makes it an ideal laboratory for the study of dispersal patterns. The first stratum of South American land mammals consists of early groups, either indigenous or of unknown origins, that radiated to fill niches and adaptive zones within the continent. By contrast, stratum 2 consists of waif dispersants that arrived across water barriers in the Oligocene. Stratum 3 shows the impact of the land bridge, with the appearance of 16 new families. Some Cricetidae and Procyonidae were included among these "walkers," although other Procyonidae, and perhaps other Cricetidae as well, certainly arrived earlier by water.

A second scenario accepts the fossil record at face value, building on the assumption that the first appearance of cricetids in the late Montehermosan marks or approximates their time of arrival (Patterson and Pascual 1972; Jacobs and Lindsay 1984). According to this scenario, cricetids either experienced an as yet undocumented radiation in southern Central America, and were thus taxonomically diverse at the time of their arrival, or they underwent an explosive adaptive radiation following their arrival in South America. If this scenario is correct, cricetids were the first North American group to walk south across the newly emerged Panamanian land bridge.

The total generic diversity of dispersant families in North and South America through time is summarized in Figure 5. In South America there was an exponential increase of genera in families that arrived from North America, whereas in North America the increase of South American immigrants was significantly lower. The possible reasons for this difference will be explored below.

Filter effects of the land bridge

All the "walkers" preserved as fossils represent taxa that were apparently tolerant of or specifically adapted to savanna ecosystems. This indicates the presence of a continuous corridor or, at the very least, a shifting mosaic of open-country habitats through the American tropics (Webb 1978, 1985). Webb points out that the southern part of the land bridge probably served as a barrier to true steppe biota throughout its existence, because no species adapted to a desert habitat are involved in any phase of the interchange. The shifting distribution of subhumid savanna ecosystems on the land bridge thus influenced the dispersal of the taxa living in them during the time of the interchange.

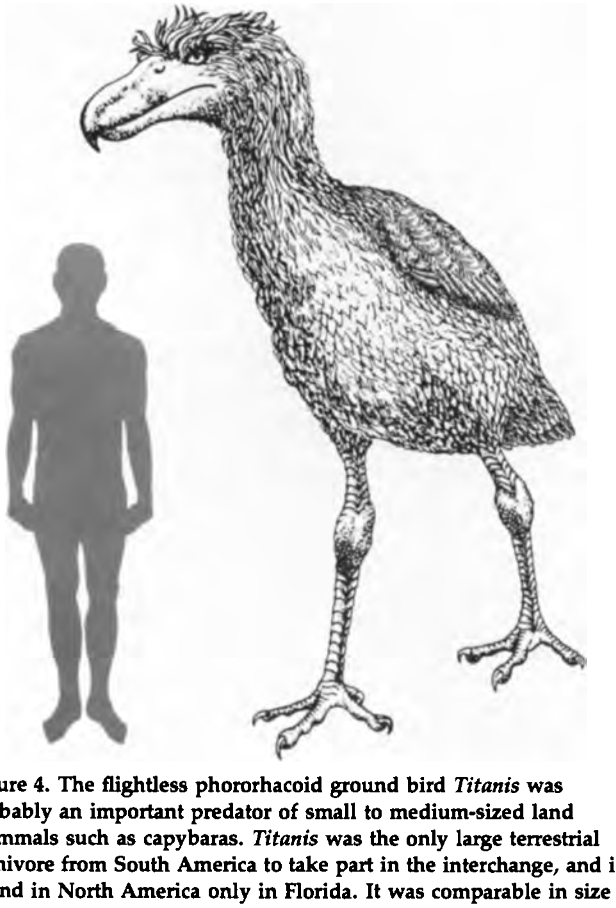


Figure 4. The flightless phororhacoid ground bird *Titanis* was probably an important predator of small to medium-sized land mammals such as capybaras. *Titanis* was the only large terrestrial carnivore from South America to take part in the interchange, and is found in North America only in Florida. It was comparable in size to *Megatherium*, attaining a height of over 3 m. A human figure is shown at the left for scale.

Man has been credited with being the sole or primary agent in a process of overkill called "blitzkrieg"

The history of savanna habitats on the land bridge has been studied in some detail (Raven and Axelrod 1975; Webb 1977, 1978). During glacial advances in temperate regions and at high tropical elevations, low areas in equatorial latitudes became cool and dry, resulting in the shrinking of wet tropical forest habitats to island-like refuges and the expansion of dryer savanna habitats (Haffer 1974; Van der Hammen 1974). The reverse occurred during times of glacial retreat. Several marine regressions occurred in the Caribbean area during times of glacial advance, providing optimal ecological windows for the reciprocal dispersal of savanna biotas between the Americas (Cronin 1981). One such regression is documented at about 3 MYA (± 0.2), another about 2 MYA, and a third about 1.4 MYA. These times approximate those of the major episodes of reciprocal dispersal as recorded in the fossil record: 2.8 to 2.5 MYA, 2 to 1.9 MYA, and 1.4 MYA. These "sister" dispersal events record the existence of savanna corridors, and explain the pulsations of interchange shown in Figure 5.

During times of glacial retreat, such as today, the distribution of savanna consists of disjunct habitats (Fig. 6). In times of glacial advance, however, these habitats would have been united by a corridor along the eastern side of the Andes—Webb's so-called "high road" or "Andean route" (1978). This corridor provided a north-south route that permitted the dispersal of savanna biotas within South America; more important, it continued across the Panamanian land bridge into the southern United States, extending eastward into Florida. In addition to creating this corridor, glacial advances were accompanied by drops of as much as 50 m in sea level, resulting in a widening of the land bridge. During times of glacial advance the savanna habitats of the southern United States and southern South America were thus mutually accessible. The principal obstacles to a complete intermingling of their biotas were distance and competitive exclusion.

Many species in South America today have populations restricted to disjunct savanna habitats, and a similar situation is found in Central America and northern South America, where some species are restricted to savanna habitats now separated by 1,700 km of wet tropical forest (Hershkovitz 1966, 1972; Webb 1985). These disjunct populations testify to the existence of the last savanna corridor between the Americas, which was in operation 12,000 to 10,000 years ago (Bradbury 1982; Markgraf and Bradbury 1982).

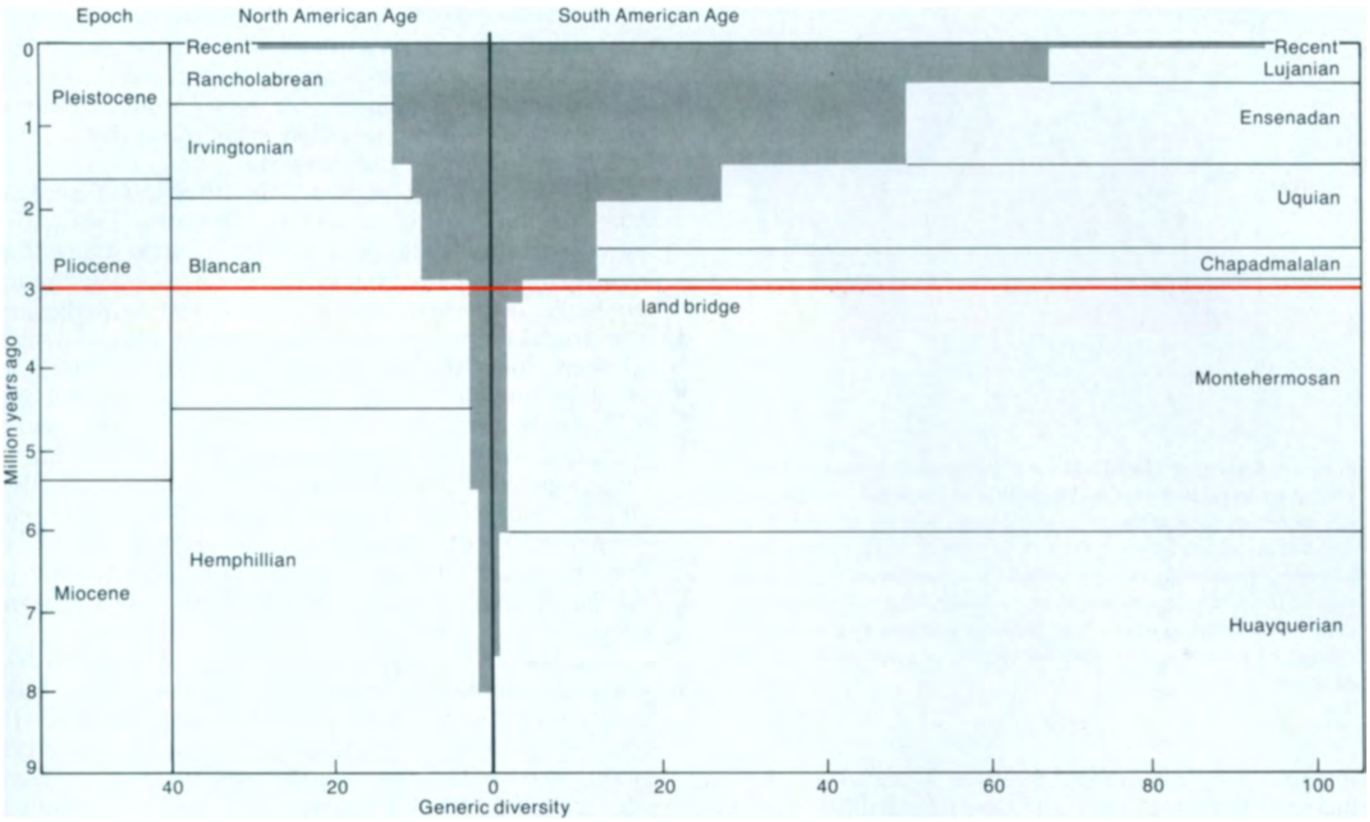


Figure 5. A comparison of the generic diversity of North and South American land mammals over the last 9 million years shows the dramatic effect of the appearance of the land bridge 3 MYA (*color*). In addition, it is apparent that in South America there was an exponential increase in genera that arrived from North America, whereas in North America the increase of South American immigrants was much lower. Four major dispersal events marked by sharp increases in diversity appear to coincide with periods of glacial advance, when the presence of a savanna corridor or a mosiac of open-country habitats may have facilitated immigration.

During the time of the interchange, recurrent glacial events thus produced a filtering effect that determined which types of animals could disperse and when. The expansion of the savanna during glacial advances has its antithesis in the expansion of the tropics in times of glacial retreat such as the present. Taxa in wet tropical forests seldom if ever leave a fossil record, and we therefore know virtually nothing about the dynamics of the interchange during such periods. Many wet tropical forest taxa are present today in both southern North America and northern South America, but we have no record of which taxa went north and which went south during the last three million years. Our understanding of the Great American Interchange is thus biased by the fact that the evidence comes only from times when the savanna habitat was at its maximum.

Faunal dynamics

The success or failure of the dispersants can be investigated by analyzing various aspects of taxonomic evolution—that is, by measuring changes in the total number of taxa or in the number of taxa within clades over time (Marshall et al. 1982; Webb 1984). MacArthur and Wilson's equilibrium theory (1967) predicts that over time a region such as a continent will become saturated with taxa, reaching a level of diversity where rates of turnover are stochastically constant. Equilibrium will then persist until it is disrupted by the appearance of new taxa, a change in physical environment, or a combination of the two.

Do the taxa involved in the interchange show evidence of turnover induced by immigration? Figure 7 shows that the diversity of stratum 1 families in South America began to decrease steadily in middle Miocene time and slightly more sharply in late Pliocene time, when stratum 3 families began to appear there in large numbers. The decrease in stratum 1 families between the middle Miocene and late Pliocene is offset by an increase in stratum 2 families, suggesting that one was being replaced by the other before the interchange began. The appearance of stratum 3 may have accelerated the decrease of stratum 1 families, but the continued decline of stratum 1 families during late Cenozoic time clearly represents a trend begun before the interchange. It is thus possible to speculate that some or most of the decrease in the diversity of stratum 1 families during the time of the interchange is unrelated to the appearance of stratum 3 groups. Among genera, diversity decreased in strata 1 and 2 in the late Pliocene and Pleistocene but increased markedly in stratum 3 during the same time. The appearance of stratum 3 groups thus resulted in only a minor increase in total family diversity but a significant increase in generic diversity.

It has been suggested that the ungulate-like taxa of stratum 1—litopterns and notoungulates—were actively

Figure 6. Recurring glacial advances and retreats appear to have played an important part in the rhythm of dispersal. In times of glacial retreat such as the present, savanna habitats contract into disjunct areas, as shown at the left; in periods of glacial advance, however, these habitats were united by a corridor along the eastern side of the Andes (*right*), providing a north-south route that extended into the southern United States and east to Florida. Arrows indicate this route and avenues of dispersal within South America.

replaced by immigrating stratum 3 ungulates, which included horses, camels, and deer (Webb 1976). However, much of the extinction of native ungulate-like taxa in South America took place before the interchange, and was thus unrelated to the arrival of stratum 3 groups (Patterson and Pascual 1972). The replacements that occurred during the interchange involved an interplay among the native ungulates, some ungulate-like caviomorph rodents, ground sloths, glyptodonts, and the immigrant North American taxa (Marshall 1981). There is no clear evidence of replacement of any ungulate group during interchange time due to rampant competition.

Among the large carnivorous groups, the doglike borhyaenid marsupials were extinct before the time of the interchange. If any competitive interaction with the invading carnivores of stratum 3 occurred, it would have been with the large flightless phororhacoid ground birds, whose extinction in South America coincides with the arrival of this group (Marshall 1977). Among mammals, the only potential example of competitive replacement is the extinction of the saber-tooth marsupial *Thylacosmilus*, which coincided with the arrival of the true saber-tooth placental, *Smilodon*.

The concept of "prey naivete" has broad implications for the mixing of faunas (Diamond 1984). The introduction of new predators in historic times has repeatedly shown that native species may be naive about predators in general and new predators in particular. The arrival of stratum 3 carnivores, "the likes of which southern ungulates had never before experienced," as Webb points out (1976, p. 225), may explain the fact that a decrease in stratum 1 and 2 ungulate-like forms coincided with an increase in immigrant stratum 3 ungulates. It is possible that the replacement of large stratum 1 and 2 herbivores by stratum 3 ungulates was passive, rather than being due to active competition. The immigrant carnivores may simply have killed off some of the native prey, making room available for immigrant prey.

At the end of the last glaciation, 12,000 to 11,000 years ago, humans migrated out of Asia by way of the Bering land bridge, passing southward through North America and into South America. Within possibly 1,000 years, man apparently occupied most or all of the New World (Martin 1973). Humans were the last stratum 3 dispersants to South America, and their arrival coincides with the extinction of most large-bodied taxa in both North and South America (Marshall et al. 1984). Man has been credited with being the sole or primary agent in this phenomenon through a process of overkill called "blitzkrieg," in which sudden extinctions followed the initial colonization of a land mass inhabited by animals that were especially vulnerable to the new human predator. The disappearance of these large-bodied species in the Americas at the end of the Pleistocene is certainly consistent with such a process, although a model based on climatic change remains a viable alternative (Markgraf 1985).

Whatever the cause, the consequences of this extinction event in South America were dramatic. Of the 37 land mammal families recorded in Lujanian faunas, 8

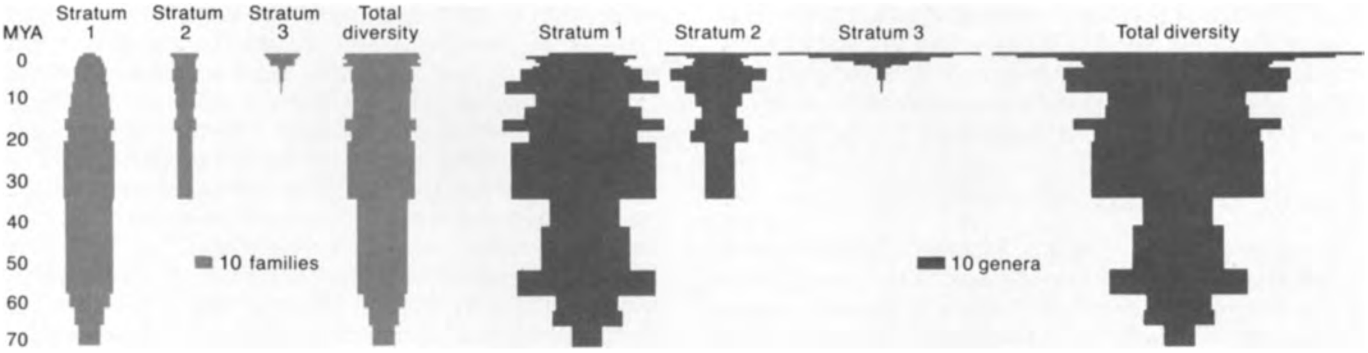


Figure 7. Spindle diagrams of family and generic diversity among South American mammals help to distinguish trends begun before the interchange from the direct effects of the land bridge. The decline of stratum 1 families visible at the far left clearly represents a trend predating the appearance of the land bridge 3 MYA, suggesting that this decrease in diversity is unrelated to the arrival of stratum 3 families. For genera, however, as shown at the right, diversity simultaneously decreased in strata 1 and 2 and increased significantly in stratum 3, demonstrating some replacement between native and immigrant taxa. (After Marshall and Cifelli, in press.)

(21%), were extinct by Holocene time, even though all 8 families included more than one genus. Of the 153 land mammal genera documented in Lujanian faunas, 56 (37%) were now extinct, including 35 belonging to those 8 families. Of the extinct genera, 54 (96%) were of large body size, suggesting that this event was selective; the taxa that became extinct were clearly not a random sample of Lujanian land mammal fauna (Marshall and Cifelli, in press).

The success of North American taxa

In evaluating the relative success or failure of North and South American interchange species, two factors must be kept in mind. First, it is necessary to distinguish true dispersants, which are represented by the same or a sister taxon on their native continent, from pseudodispersants, which are derived from true dispersants. Just because a genus belongs to a family that dispersed from another continent, it does not follow that it itself dispersed. For example, the elephant-like gomphothere *Cuvieronius*, a true dispersant to South America, is known from pre-interchange faunas in North America. After reaching South America it gave rise to *Haplomastodon* and *Notiomastodon*, which are pseudodispersants; although they belong to a family that dispersed from North America, they themselves evolved in and are endemic to South America (Webb 1985). Such pseudodispersants must be identified and factored out when analyzing dispersal events. Second, the number of potential dispersants is directly related to the size of the source faunas. A larger geographic area will predictably have more taxa and hence more dispersants than a smaller area. This, too, must be taken into account.

Of the members of South American families that walked to North America, all 38 may be regarded as true dispersants, indicating that little or no diversification occurred after their immigration. By contrast, of the North American walkers (including cricetids) only 47 can be regarded as true dispersants, whereas 72, from 8 families, represent pseudodispersants. Thus about 60% of the North American genera in South America apparently evolved in situ on that continent, demonstrating that these immigrants experienced considerable diversification after their arrival.

The total surface area of North America and Central America (24 million km^2) is greater than that of South America (18 million km^2). This fact, along with the known fossil record, explains why North America had an average of 60% greater generic diversity and hence more potential dispersants than South America during the time of the interchange (Marshall et al. 1982). When the differences in the size of the source faunas are taken into account and only true dispersants are considered, the interchange can be seen to be balanced, with the number of true dispersants proportional to the size of the source faunas in both continents. More taxa dispersed to South America than to North America simply because there were more potential dispersants in North America.

This aspect of the interchange is predicted by equilibrium theory. However, the later explosive diversification of true dispersants in South America as opposed to North America is unique and asymmetrical. Several theories have been proposed to explain this difference. The classic view during the first half of this century was that the taxa of North America were competitively superior to those of South America. This view was founded on the belief that the taxa existing in North America at the beginning of the interchange were the survivors of numerous earlier invasions and thus tested and "worldly wise," possessing such varied advantages as more rapid reproductive rates, narrower niche selection, and more rapid evolutionary responses to new opportunities (Webb 1985).

A more recent view, compatible with this, sees the North American taxa as "insinuators" able to exploit niches and adaptive zones not occupied by native South American taxa (Patterson and Pascual 1972; Hershkovitz 1972). Thus the North American immigrants would not have competed directly with South American natives, but were able simply to radiate and fill unoccupied space. Another theory holds that ongoing geological activity created new habitats and changed the old ones, resulting in the extinction of some native taxa before and during the time of the interchange. The opening of niches and adaptive zones through the disappearance of prey-naive natives would have allowed the North American immigrants to disperse into ecological vacuums. These features would have facilitated both the arrival of true dispersants and their radiation into pseudodispersants. This theory implies that the changes which took place in the composition of the South American land mammal fauna were due primarily to passive replacement, and that the North American groups were simply timely invaders.

Nearly half of the families and genera now on the South American continent belong to groups that emigrated from North America during the last three million years

A fourth theory combines aspects of all these views, suggesting that the two principal evolutionary theaters for the interchange were not South and North America but South America on the one hand and North America and Eurasia on the other (Webb 1985). This theory stresses the imbalance between the area available to northern taxa adapted to temperate conditions and that available to the southern taxa, and holds that the presence of a vast Holarctic staging area rather than any

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inherent biological superiority explains the greater success of northern taxa after the interchange.

Although the reasons for the success of the North American immigrants remain debatable, the impact on South America is undisputed. When the interchange began about 7.5 MYA, about 60% of the South American families derived from stratum 1 and 40% from stratum 2; 70% of the genera came from stratum 1 and 30% from stratum 2. Today the composition of South American land mammal fauna is quite different: 19% of the families come from stratum 1, 37% from stratum 2, and 44% from stratum 3; 17% of the genera derive from stratum 1, 29% from stratum 2, and 54% from stratum 3. These data firmly demonstrate that the Great American Interchange resulted in a major restructuring. Nearly half of the families and genera now on the South American continent belong to groups that emigrated from North America during the last 3 million years.

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