era to pass in both directions. This was the Great American Biotic Interchange. Before looking more closely at the many kinds of vertebrates that joined in the reciprocal northward and southward dispersals between the Americas, it is important to specify the exact timing of this remarkable event.

When Did the Interchange Begin?

The question of when the land bridge between the American continents was completed has been answered in various ways by different disciplines. Before comparing dates, therefore, one must consider carefully what is being dated. Jeremy Jackson and Luis D'Croz, studying the marine seaway, date strata in which marine organisms diverge and reflect shallowing and severing of interocean continuity and also upwelling of adjacent currents. Predictably, these disruptions of the formerly broad and deep portal between the Atlantic and Pacific must precede establishment of a complete isthmian land bridge across the former seaway. Logically, one would expect the earliest dates leading up to the land bridge to come from deep-water marine separation, then shallow-water settings, and finally from terrestrial connections between North and South America.

These expectations are borne out by the data from independent disciplines. For many years the marine separation dates, ranging between 3 and 4 million years ago, were widely quoted. The younger dates for establishment of the land bridge, about 2.5 million years ago, were derived from land mammal dates and were often thought to be too young because they were only about half as old as the oldest marine-derived dates. Taken together, these dates reflect the whole history of the closing seaway and the emerging land bridge.

The terrestrial dates for completion of the land bridge are based not only on fossil evidence from Central America, but also on a broad sample of dates wherever the waves of new immigrants appeared in North and South America. At present the most precise chronology dating immigrants that surely crossed the isthmian land bridge can be found in the western United States. In southern California, where the San Andreas fault passes through the Salton Sea basin and into the Gulf of California, active rifting provides a rich geological section of marine and terrestrial sediments. The Imperial Formation of late Pliocene age (about 3.5 to 2 million years ago) includes tropically adapted monk seals and many warm-water invertebrates that had continuity from the Atlantic through Panama's marine portal to the Pacific Ocean and then

north to what is now southern California. Just above the Imperial Formation, however, in slightly later Pliocene terrestrial deposits, occur diverse immigrant land animals from South America, including armored tank–like glyptodonts, armadillos, more sloths (not closely related to the ground sloths that came earlier), capybaras (large aquatic rodents still living in the tropical lowlands), and porcupines (another group of South American rodents related to guinea pigs). Thus, the late Pliocene emplacement of the Central American land bridge is well documented in southern California

A similar suite of immigrants from South America is very precisely dated with volcanic ash dates and magnetic reversal chronology in southern Arizona in an area known as 111 Ranch. There, the best dates just below and just among the first evidence of immigrant animals from South America are about 2.4 million years ago.

In Central America, the best-dated section that gives evidence of new immigrants from South America occurs in the ancient lake beds near Arroyo del Sísmico in El Salvador. There, fine-grained ashy sediments of late Pliocene age delicately preserve many kinds of fossils, including such aquatic microorganisms as diatoms and ostracods (tiny bivalved crustaceans), and also plant impressions, fish remains, the whole skeleton of a rare mustache bat, and diverse large mammals, among them two previously undescribed kinds of ground sloths.

Similar dates for immigrant land animals occur in South American sites. The great sea cliffs southeast of Buenos Aires provide an excellent sequence of late Pliocene and early Pleistocene sediments full of land mammal fossils. There, the first evidence of groups derived from North America, including llamas, horses, sabercats, bears, peccaries, and field mice, appears in the very late Pliocene. The best dates fall rather close to 2.4 million years ago, just as they do in western United States and Central America.

Earlier evidence of terrestrial immigrants moving between the two American continents may be found. Until that happens, however, the sites just enumerated give an excellent approximation of the time the great interchange began. The time elapsed while several animal species spread through Panama northward to Arizona, in the absence of major barriers, is almost instantaneous in the perspective of geological time. The great speed of immigrant mammals is exemplified by rabbits, which, introduced into Australia for the sport of hunters, spread over the entire continent within a few decades. Although the search for earlier contact continues, an abundance of evidence throughout the New

World places the first rush of interchange animals through the isthmian area at about 2.4 million years ago.

Which Species Were Involved in the Interchange?

Once the land bridge was established, an extraordinary crossing of many terrestrial animals began in both directions. The most comprehensive fossil evidence comes from land mammals because they are generally abundant and their teeth, which fossilize particularly well, make possible rather precise identifications, usually to species level. A general accounting of families that are recorded on both sides of the land bridge in the late Pliocene and early Pleistocene is given in tables 4–1, 4–2, 4–3. Most of these groups are known to have extended their geographic ranges right through the tropics and into temperate latitudes of the opposite continent. Llamas, for example, which have Miocene and early Pliocene records only in North America, are found (suddenly) in the late Pliocene in the southern semidesert terrain of Patagonia. Equally remarkable is the widespread distribution of the ground sloth *Megalonyx*, which reached both coasts of North America and as far north as Alaska.

Can one infer from this roster of families that crossed through Panama what the land bridge was like ecologically at the time the bridge formed? Most groups were grazers (eating grasses and other coarse, low herbs) that lived in large herds and are best known in settings of open woodlands or grassland savannas. Horses and llamas are two of the most familiar examples from North America. From South America, toxodonts (large rhinoceroslike ungulates), diverse ground sloths, and glyptodonts (shelled relatives of armadillos with massive plant-grinding jaws and teeth) suggest similar ecological settings. Some herbivorous mammals of the interchange were browsers or mixed feeders, but a majority were grazers.

Not all interchange mammals were herbivores, however. Six families of carnivores entered South America via the land bridge with devastating effect on the native herbivore populations, which had absolutely no experience with efficient mammalian carnivores. Within a geological instant after the interchange began, a richly mingled fauna ranged widely from the Great Plains of North America to the Pampas of Argentina and was surely well adapted to temperate grassland savanna and to open woodland. Thus, both continents were faunally enriched by the late Pliocene interchange.

Central America hosted a particularly vital mixture of new immi-

Table 4–1. Mammal Families of the Great American Faunal Interchange

Legions of the *North*	
Scientific Name	Common Name
Soricidae	shrews
Leporidae	rabbits
Heteromyidae	pocket mice
Geomyidae	pocket gophers
Sciuridae	squirrels
Cricetidae	field mice
Felidae	cats
Mustelidae	skunks and otters
Canidae	foxes
Procyonidae	raccoons
Ursidae	bears
Gomphotheriidae	mastodonts
Tapiridae	tapirs
Equidae	horses
Tayassuidae	peccaries
Camelidae	llamas
Cervidae	deer

Table 4–2. Mammal Families of the Great American Faunal Interchange

Legions of the *South*	
Scientific Name	Common Name
Didelphidae	opossums
Dasypodidae	armadillos
Chlamytheriidae	giant armadillos
Glyptodontidae	"tanklike" edentates
Megalonychidae	bear-sized ground sloths
Mylodontidae	middle-sized ground sloths
Megatheriidae	elephant-sized ground sloths
Bradypodidae	three-toed tree sloths
Myrmecophagidae	anteaters
Callithricidae	marmosets
Cebidae	monkeys
Hydrochoeridae	capybaras (large aquatic rodents)
Erethizontidae	porcupines
Caviidae	guinea pigs
Agoutidae	pacas
Dasyproctidae	agoutis
Echimyidae	spiny rats
Toxodontidae	rhinoceroslike ungulates
Phororhachidae	giant predaceous birds

Table 4–3. Families Which Go Extinct in the Pleistocene of Central America*

Chlamytheriidae
Glyptodontidae
Mylodontidae
Megatheriidae
Hydrochoeridae
Gomphotheriidae
Elephantidae
Equidae
Camelidae
Bovidae

*Some groups listed here survived in South America. In addition many genera (e.g., *Smilodon*) became extinct, but they are not listed if their family (e.g., Felidae) survived in Central America.

grant animals extending their ranges in both directions. Scientists cannot specify what the crossroads were like ecologically in the late Pliocene, but it is clear that the interchange landscape included a wide range of both forested and unforested habitats, offering a broad ecological avenue to many kinds of land animals.

The many large herds of grazing and mixed-feeding herbivores themselves had a strong ecological impact on Central American landscapes, as do the vast herds of ungulates in the tropical and subtropical savannas of Africa today. Massive annual migrations, then as now, allowed diverse groups to alternate grazing on coarse fodder with mixed feeding and browsing on forest margins during the most favorable seasons. Such high activity undoubtedly kept all but the densest rain forest more open than at present. Modern tropical ecologists point out that the large fruits of palms and guanacaste trees require large herbivores to crack and disperse them. Horses, reintroduced by the Spanish, are the only competent seed-cracking herbivores at present. One can only guess at the elaborate interactions that must have occurred between large herds of herbivores and tropical American vegetation during the Pliocene and Pleistocene.

Paleontological evidence of the interchange throughout North, Central, and South America suggests that diverse species extended their ranges rapidly and then stabilized in the early Pleistocene. Most families that migrated had done so during the late Pliocene or early Pleistocene. According to the North American record, the last straggler was the opossum, which arrived in Florida in the mid Pleistocene, just over 1 million years ago. Horses, camels, sloths, peccaries, toxodonts, and many others had crossed reciprocally through the tropics and lived in both American continents by about 2 million years ago.

Recent animal distributions, as well as some late Pleistocene fossil evidence, suggest that there was a second, ecologically different phase of the interchange, one in which Central America played a decisive role. The second phase involved a different cast of characters, animals that were more specifically adapted to equatorial lowland rain forest environments. They did not extend their ranges into high temperate latitudes on either side of the equator. These animals moved mainly from the vast domain of the Amazon basin northward throughout the lowlands of Central America, reaching their northernmost limits along the Caribbean coast below the tropic of Cancer, in the general area of Veracruz, Mexico. This second stage of intertropical faunal movement is represented among birds by parrots, toucans, and guans (arboreal, tropical turkeylike birds), and among tropical butterflies by the magnificent iridescent *Morpho* and the colorful *Heliconius*. Tropical mammals that moved from Amazonia to Central America include tree sloths, large lowland rodents such as agoutis and pacas, and a myriad of monkeys.

The wealth of tropical biota that moved northward into Central America in this second wave of the interchange shifted the dominant faunal characteristics from North American temperate to South American tropical. And that is why the great nineteenth-century naturalists such as Charles Darwin, Alfred Wallace, and Joseph Hooker, in surveying the New World's rich terrestrial fauna and flora, linked the Central American tropical biota closely with the Amazon biota, placing them together in the *Neotropical Realm*. All subsequent biological surveys and studies of the American tropics have confirmed the validity of this Neotropical affiliation. Only geologists and paleontologists are aware of the earlier close linkage between North and Central American land life and its total separation by a deep-sea barrier from South American lifeforms.

Paleontologists can confirm this second intertropical phase of the interchange mainly by negative evidence. Some large grazing animals from North America that might have been expected to cross the isthmian land bridge into South America did not do so because they came too late (see below). These include pronghorn antelopes, mammoths, and the American bison. The earliest bison (also known as buffalo) entered North America from Asia in the late Pleistocene and spread widely not only throughout the grasslands of the midcontinent but also into open woodlands in the east and southeast. Bison herds also spread southward into Central America, following thornscrub and savanna

habitats along the Pacific slopes of El Salvador, Honduras, and northern Nicaragua. Indeed, some remarkable footprints of bison and early humans are preserved on the surface of an ancient lava flow where the lava and the fleeing creatures entered the northern edge of Lake Nicaragua. However, bison were not present in Central America early enough in the Pleistocene to spread southward through the more open environments that may have prevailed then. Evidently they were too late: the mesic climate and massive rain forest prevented them from reaching southern Central America and crossing the land bridge. Such a conclusion coincides with Paul Colinvaux's evidence (see chapter 5) that in the later Pleistocene lowland rain forest throughout Panama presented a massive barrier to open-country animals.

Several biological lessons inhere in the subsequent history of groups that participated in the interchange. In general, the groups that spread southward into South America had a long, wide-ranging history not only in North America but also, before that, in Asia. They were in some sense already successful in spreading through a wide range of latitudes from one continent to another. And most of these groups from the north became very successful, by spreading widely and diversifying greatly after they had entered South America. Groups extending their ranges in the opposite direction (into Central and North America) had no other continental experience, having been isolated in South America by ocean barriers. The following examples will show that they had very limited success, undergoing virtually no diversification and only one or two wide distributions.

Animals That Spread Northward

Megalonychid Ground Sloths

These bearlike animals were one of six families of sloths that evolved in South America during its long isolation from other continents. Their cousins, the much smaller tree sloths, still survive hidden in the upper canopy of equatorial rain forests in Central and South America. Four distinct branches of ground sloths, including megatheriids such as *Eremotherium* (fig. 4–2), which were much larger than megalonychids, reached North America. But the megalonychids came first and spread widely. As stated above, some megalonychids were the first to cross narrow water barriers about 8 million years ago, anticipating by more than 5 million years the construction of a complete isthmian land bridge. Descendants of these sloths spread more widely throughout temperate North America than any other immigrant group from South America. In the late Pleistocene they occur as far north as Alaska and in almost every state in the contiguous United States. President Thomas Jefferson was intrigued by those that reached Kentucky and were discovered at Big Bone Lick when that was a frontier area. That large, late Pleistocene species was named *Megalonyx jeffersoni*. The largest megalonychid occurred much earlier in Central America. That rare sloth is *Meizonyx salvadorensis*, a primitive form with narrow, pointed canine teeth from a very late Pliocene site at Arroyo del Sísmico in El Salvador. Unfortunately, all of the ground sloths throughout the Americas became extinct at the end of the Ice Age. President Jefferson had hoped that Lewis and Clark would find some when they explored the western wilderness and specifically instructed them on that mission. Today there are few places remote enough to look for living examples of such large animals.

The Giant Anteater

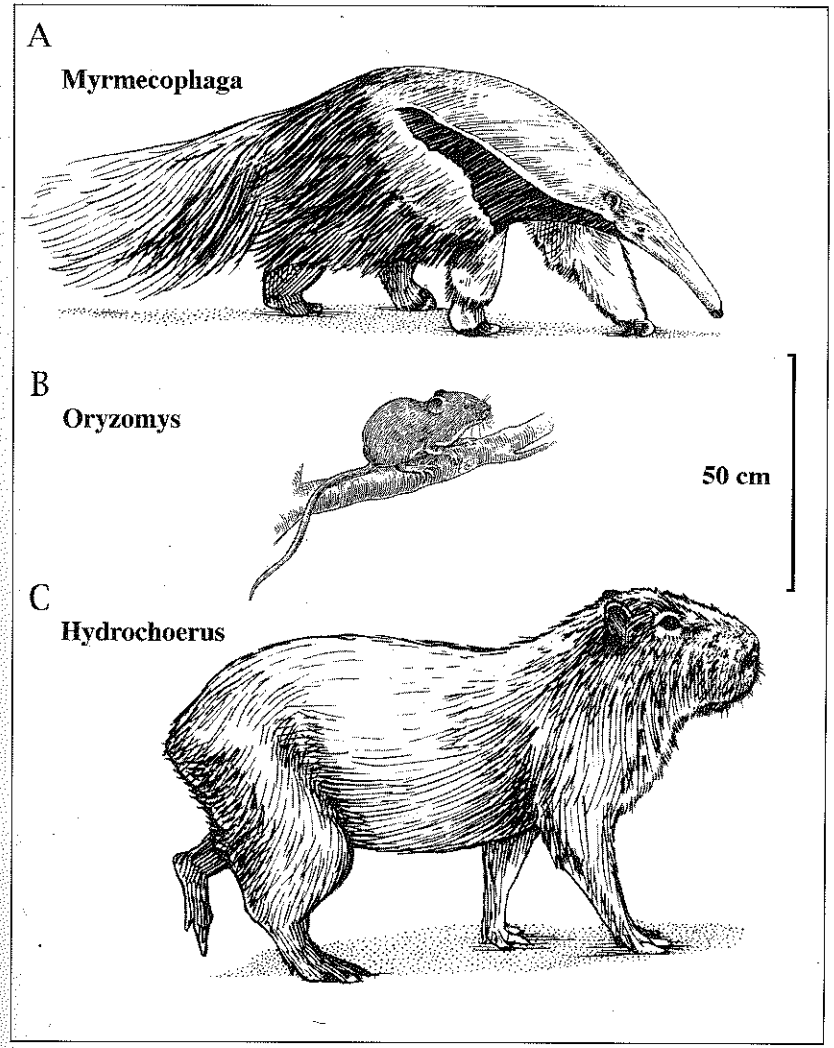
One of the most distinctive families of large mammals that evolved in South America consists of three genera of anteaters. The biggest and most distinctive of these is the giant anteater, with the scientific name *Myrmecophaga tridactyla* and the equally appropriate Spanish popular handle, *oso hormiguero* (*oso* = bear, *hormiga* = ant) (fig. 4–3A). Nearly every feature of its anatomy and behavior is specialized for its unusual diet, which consists exclusively of termites from large terrestrial mounds that develop abundantly on fallen trees and tree roots in tropical American savannas. Among the giant anteater's peculiar adaptations are its powerful claws, short, heavy limbs, long hair, extremely long tongue, and tubular jaws with no teeth. Early fossil records of almost modern myrmecophagids come from Brazil, Uruguay, and Colombia about 15 million years ago. Of course, none are known in North or Central America until after the land bridge allowed their northward progress. Then clear-cut evidence shows that *Myrmecophaga* shuffled and ate its way clear through the American tropics in time to be fossilized in a 1.5-million-year-old site known as El Golfo in the northwestern corner of the state of Sonora, Mexico. This fossil antbear reached about 3000 miles north of its nearest living relatives, which now occur in the tropics of eastern Guatemala and southern Belize. The present climate in this part of Sonora is too arid and too cold in the winter to support the tropical forests that sustain an abundance of large termite nests, which is the only food that can sustain a population of

4–2. The giant ground sloth *Eremotherium* scaled to a human 2 meters tall. Sloths are migrants from South America.

giant anteaters. The giant anteater ranges southward into northern Argentina.

Armadillos

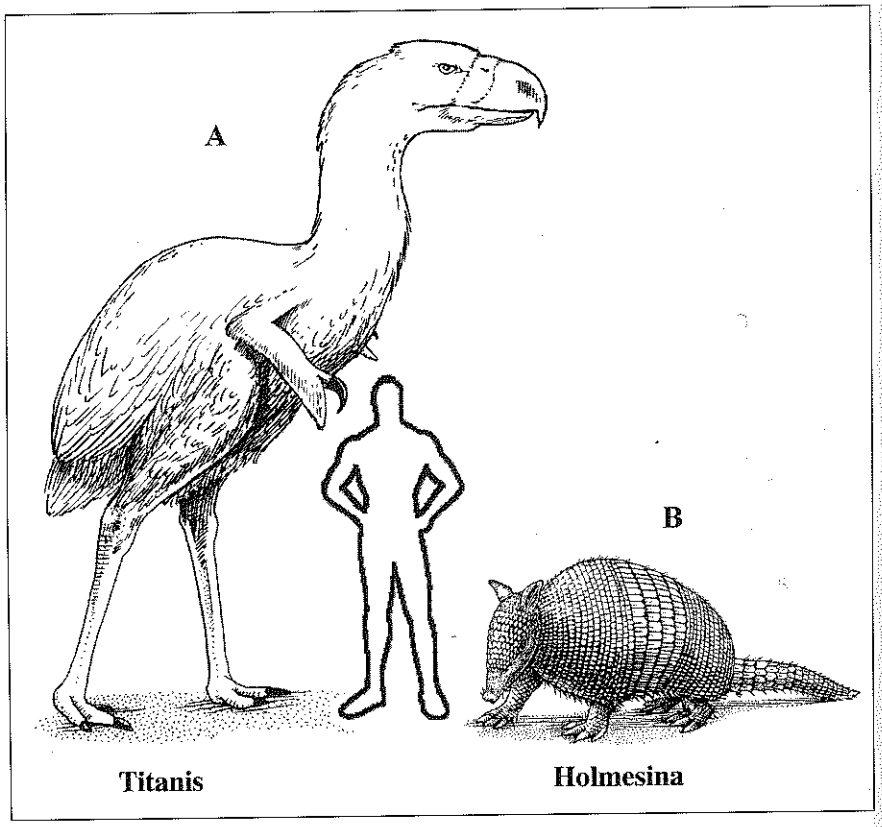
One of the South American groups that repeatedly extended its range northward into Central and North America was the armadillo family. Perhaps their shells protected them from unaccustomed predators, and perhaps their broad range of acceptable diets, including insects and other small animals, carrion, tubers, fruits, and other plant parts, helped



4–3. (A) The giant anteater *Myrmecophaga,* a southern migrant; (B) *Oryzomys,* a rice rat, one of the vast variety of the mice family that proliferated in South America after migrating from the north; (C) *Hydrochoerus,* the giant capybara rodent, evolved from migrants from the north.

them survive in all but the most arid environments. The only modern species in temperate North America (north to Oklahoma and Kansas) is *Dasypus novemcinctus* (the nine-banded armadillo), but several other extinct relatives reached equally far north in the late Pliocene and Pleistocene. In Central America the nine-banded armadillo is joined by the naked-tailed armadillo, *Cabassous centralis.*

One of the largest and most impressive of the extinct relatives of armadillos was *Holmesina,* the tanklike form with a shell nearly four feet in diameter (fig. 4–4B). Glyptodonts specialized in eating plants and plant roots and had much deeper jaws and more powerful cheek muscles than any living armadillo. Some specimens show a deep stab wound into their skulls, indicating that they were hunted and killed by saber-toothed tigers. In spite of this evidence that some individuals were mortally wounded, the glyptodonts were among the first species to cross the land bridge and establish themselves abundantly throughout North and Central America. On the other hand, their importance may be somewhat exaggerated because their massive shell elements are easily preserved, discovered, and identified.



4–4. (A) *Titanis,* the spectacular, giant, carnivorous bird scaled to a 2-meter human. A migrant from the south, they are found fossil as far as Florida in North America; (B) *Holmesina,* one of the giant armadillos, is also a southern emigrant.

Toxodonts

Most of the large herbivorous animals that had evolved in South America vanished before the interchange or were vanquished by competition from such northern immigrants as horses, camels, and tapirs. One notable exception, however, was the toxodonts, a kind of rhinoceroslike group of very large herbivores (figure 4–5A). The name *toxodont* refers to their curved upper teeth, which formed a powerful battery of tall grinders, well equipped to masticate large volumes of leafy material. These large herding herbivores actually extended their ranges northward against the tide, as it were, of northern ungulates moving south. The species *Mixotoxodon larensis* has been found in late Pleistocene deposits in every Central American country, usually in association with mastodons, giant ground sloths, and horses.

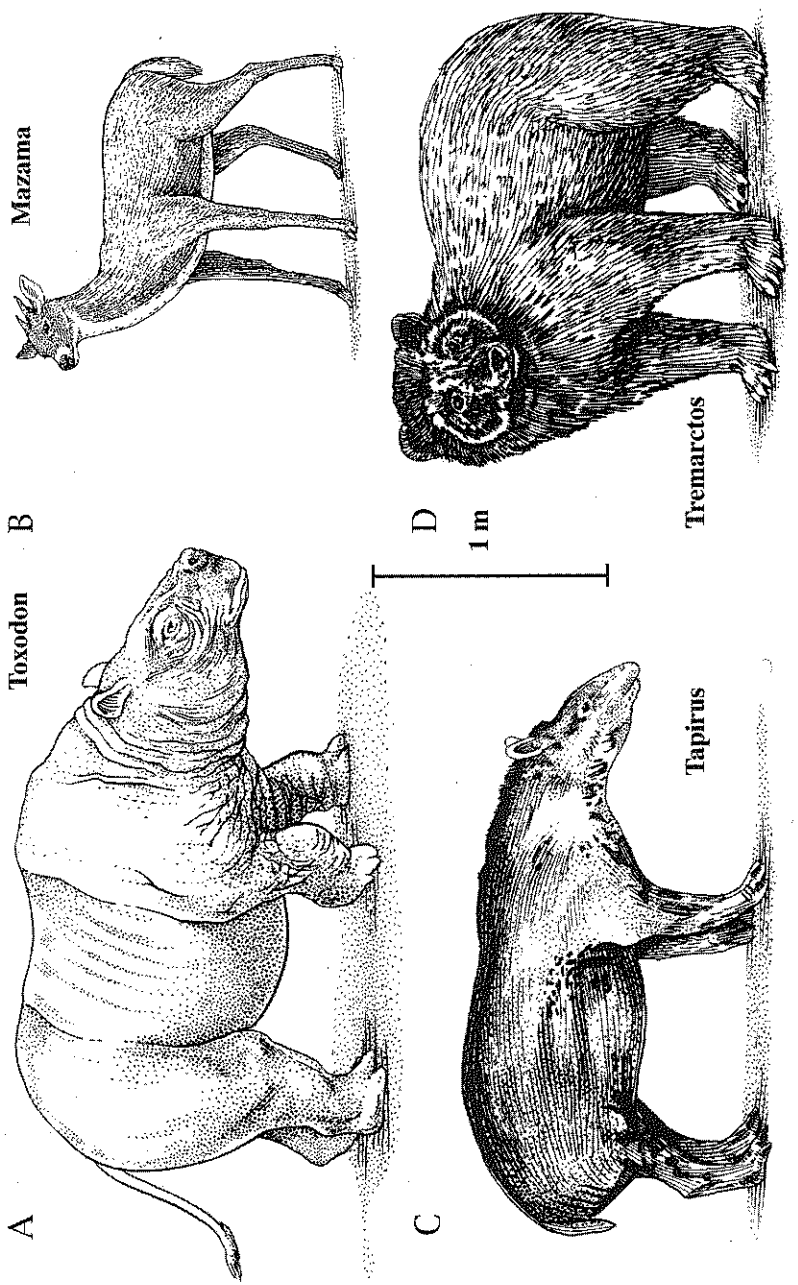
Giant Birds

A most unexpected South American participant in the interchange is a gigantic predaceous bird known as *Titanis walleri* (see fig. 4–4A). When the first fossilized toe and claw bones were discovered in the bottom of Florida's Santa Fe River they were thought briefly to belong to a dinosaur. Indeed, their powerful hind feet for running and tearing prey and their large size (more than three meters tall) closely resemble those of some dinosaurs. Their presence in late Pliocene sediments along with sloths and glyptodonts, however, indicated that they must be compared with large birds, and when scholars turned their attention to South America possibilities they quickly discovered that *Titanis* was a new genus belonging to the extinct family Phorusrhachidae from Brazil and Argentina. In recent years many more parts of this remarkable predaceous bird have been discovered in Florida, including its meat-cleaver beak. Evidently members of this group followed some of their traditional prey (such as glyptodonts) northward through the savanna corridors of tropical South America and Central America for a distance of more than 10,000 kilometers.

Animals That Spread Southward

The Cat Family

Before the land bridge formed, when South America was still an isolated continent, it had no efficient mammalian carnivores. The giant birds, discussed above, were the major large predators in open-country



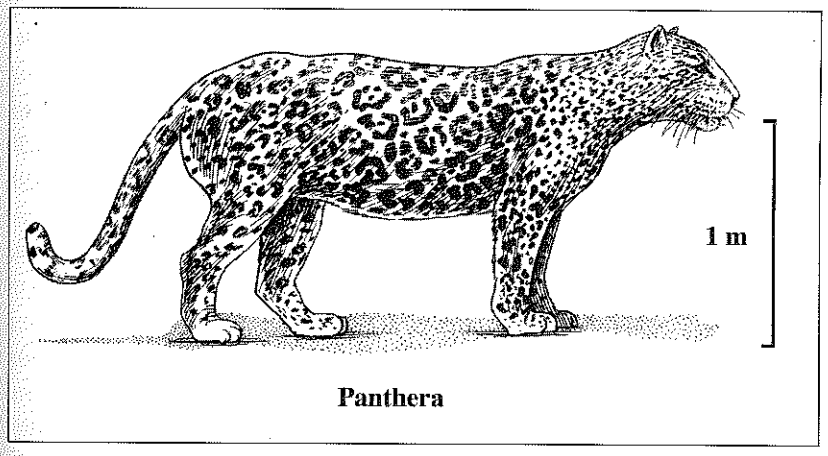
4–5. (A) *Toxodon*, a large herbivorous animal from South America that resembles a rhinoceros; (B) *Mazama*, one of the many distinctive deer that evolved in South America after migrating from the north in the interchange; (C) *Tapirus*, a well-known herbivore in Central America and the Amazon that evolved from North American stock; (D) *Tremarctos*, the bespectacled bear distinctive of the American tropics and descended from northern emigrants.

habitats, while crocodiles were active in aquatic settings. It is not surprising, therefore, that when efficient, warm-blooded mammalian predators entered South America they became widespread and successful in virtually all habitats.

This discussion focuses on the cat family, but four other carnivore families, bears, dogs, weasels, and raccoons, also extended their ranges through Central America, crossed the land bridge, and reached South America. All of these carnivore families except the bears include a considerable diversity of living genera and species in the American tropics, probably representing multiple dispersals. The bears are represented in the interchange by the spectacled bear, which still lives in tropical south America.

Both large and small members of the cat family (Felidae) prospered in the new southern continent. A surprising number of small species coexist in South America, including margays, ocelots, jaguarundis, little spotted cats, and also *Felis guigna, geoffroyi*, and *colocolo*. Many are grouped under the popular name *tigrillos*. Most, if not all, of these small felids had already originated in North America before the land bridge was formed. It is likely that margays, ocelots, and little spotted cats, which specialize in tropical arboreal habitats, had already developed in Central America. They were thus ideally positioned to spread southward when the land bridge formed.

The two largest American cats are the puma and the jaguar (fig. 4–6). There is also the rare Andean cat *Felis jacobita*. The jaguar (*Pan-*



4–6. *Panthera*, or jaguar, the largest of the tropical American cats. Cats diversified into many species in Central and South America after the interchange.

thera onca) is the largest American cat and much admired for its magnificent glossy, spotted coat. Its coat is reminiscent of a leopard's in the Old World and is similarly adapted to camouflage the large cat not only during the day in shadowy jungle settings, but also at night when it does most of its stalking. As fossils, jaguars are known in Florida, where the largest individual skulls are known, and from the time of the interchange into historic times they ranged from southwestern United States into northern Argentina. They are now restricted to large areas of fairly dense vegetation.

The puma (*Puma concolor*), on the other hand, ranges through virtually all habitats in the Americas and extends from extreme northern to extreme southern latitudes. Before the land bridge formed, both panthers and jaguars lived in Central America. Less than 3 million years ago, the land bridge offered them major new opportunities in South America. Jaguars extended their ranges through the Amazon basin into Argentina and Uruguay, while panthers covered the whole new continent.

South American Deer

One of the most successful groups of large mammals to go south is the deer family. Deer originated in the north temperate latitudes of Eurasia some 20 million years ago. They were browsers and mixed feeders that lived on forest margins. About 5 million years ago distant relatives of the white-tailed deer reached the Bering Strait, while it was still forested, and entered North America. During the Pliocene they reached Central America and there diversified. Until then, deer had never reached tropical latitudes. Important new branches of the deer family that originated in Central America were the red and brown brocket deer (genus *Mazama*) (fig. 4–5B), characterized by small body size and simple spike antlers. Another new group of North American deer developed moderate body size and short, powerful legs as an adaption to mountain dwelling. They included an extinct genus from western North America known as *Navahoceros* and the living Andean deer (*taruca* and *huemul*) with the scientific name *Hippocamelus*. The name reflects the uncertainty of its original describer as to whether it was a horse or a camel; imagine how surprised that early scientist would be to learn that he had named a deer living in the southern hemisphere. When lowland rain forest closed in the isthmian corridor, the former continuity between the short-legged deer *Hippocamelus* to the south and *Navahoceros* to the north was broken.

After the interchange still other new kinds of deer arose in South America. The surviving examples range from the diminutive *Pudu* c Andean forests through *Ozotoceros,* the pampas deer (similar in size and general appearance to the white-tailed deer), to the immense marsh deer (*Blastocerus dichotomus*) of moist tropical and subtropical habitats. And these new kinds of native deer were accompanied by immigrant groups like the white-tailed deer and the brockets from Central America. Thus, thanks to the interchange, South America changed from a continent with no deer to the continent with the most kinds of deer.

An Explosion of Mice

Even more successful than the deer family were the mice of the family Cricetidae. Before the interchange there were none in South America; today there are some sixty species in at least forty genera (see fig. 4–3B). Unquestionably these mice crossed the isthmian land bridge as part of the interchange, but their subsequent success is so astonishing that many biologists have questioned the timing of these events. How, they ask, could these mice have developed so many branches? Some are terrestrial, some arboreal, some pastoral (grazing), some sylvan (browsing), and one group (subfamily Ichthyominae) is uniquely adapted to catching fish in Andean streams. Paleontologists, constrained by the age of the land bridge, suggest that these mice experienced much of their diversification in Central America before the land bridge formed. At least six different branches (subfamilies) of the family Cricetidae are known as fossils in the late Miocene and Pliocene of subtropical North America, and many of them resemble their living South American descendants. This means that the time available for attaining the immense diversity of mice now seen in South America was about 9 million years (since the late Miocene), more than three times longer than the time available since the land bridge formed. Many cricetid adaptations to tropical conditions were probably developed in Central America, a fortuitous staging place for their subsequent peregrinations in South America.

What Has Happened to the Animals of the Interchange Today?

I have examined some examples of the many groups that crossed in both directions when the interchange took place. Most groups that reached South America were successful in the sense that they spread widely and diversified, some considerably. Fully half of the land mam-

mal genera living in South America today came from ancestors that crossed the land bridge from Central America less than 3 million years ago, and the same is true of the tropical fauna of Central America.

On the other hand, the temperate North American fauna is decidedly lacking in any strong carryover from South America. Only three mammal species from the interchange remain north of the tropics, namely, the opossum *(Didelphis virginiana),* the nine-banded armadillo *(Dasypus novemcinctus),* and the porcupine *(Erethizon dorsatum).*

In many respects, however, the success of South America mammals in temperate North America has been concealed today by a vast cataclysm (see below) that caused the extinction of most large mammals at the end of the Ice Age. This loss is much greater with respect to South American mammals than to North American forms. All of the great ground sloths and their shelled cousins the giant armadillos and glyptodonts suddenly vanished in North America, as they did in South America. Likewise, the giant amphibious rodents known as capybaras (see fig. 4–3C) disappeared from North and Central America, where they had been abundant. The great toxodonts from South America had become well established in Central America but vanished along with all of South America's native ungulate stocks at the end of the Pleistocene.

Several families of North American ungulates were also devastated by late Pleistocene extinctions, but there were nevertheless numerous survivors, many of them in the American tropics. All the species of horses and of mastodonts in North and South America were lost. Llamas, peccaries, and tapirs and jaguars were exterminated in temperate North America, although they survived in tropical America and temperate South America.

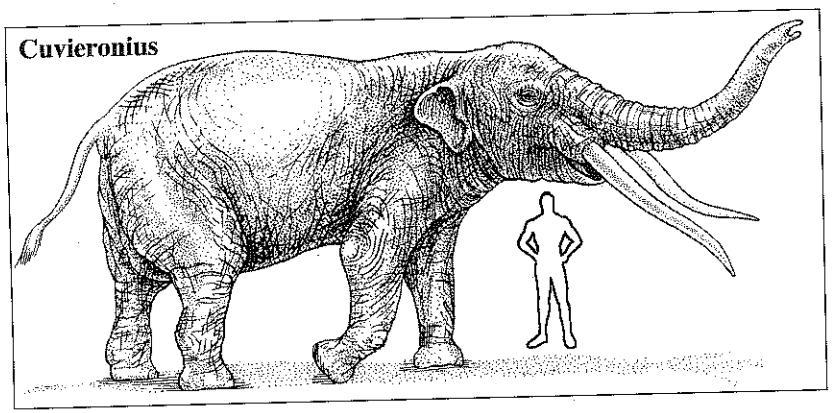
What caused these late Pleistocene extinctions? They had little effect on smaller-sized mammal groups. The main impact was on large herbivores. Most carnivores survived. For example, among the cat family all but one kind still survive. One might have predicted extinction for pumas and jaguars because so many large game animals that were their prey disappeared late in the Ice Age. This implies that they may have relied more on deer and peccaries than on the many extinct kinds of large herbivores, such as horses and mastodonts. The one genus of large cats that became extinct were the sabercats (genus *Smilodon*). Their demise was surely predictable. The South American species had become extremely large during the Pleistocene. Such sabercats were bound to become extinct throughout the Americas when most of their large prey species died out.

American paleontologists and archaeologists have proposed tw hypothetical causes of the mass extinctions of large mammals at the end of the Pleistocene. One hypothesis points to sweeping climatic changes that took place at the end of the last glacial epoch. The other implicates the hunting peoples who entered the New World and spread rapidly throughout the Americas. Both climatic events and the spread of humans correlate well with the time of mass extinctions. Dozens of kinds of large mammals, including ground sloths, horses, camels, mammoths, and mastodonts, disappeared almost at the same instant (geologically speaking), about 11,000 years ago. These extinctions may well have resulted from the combination of climatic shifts and human impacts.

The Role of Early Humans

Direct evidence of late Pleistocene animals being killed and butchered by human hunting is extremely rare in the New World. Most of the early records of Paleoindians throughout the Americas consist of lithic elements, predominantly fluted points like the classic Clovis and Folsom points (see chapter 6). Although these points were used in most instances to spear food, the lithics by themselves offer very little evidence of what species were hunted and how they were utilized.

Only a few dozen sites throughout the Americas provide ancillary evidence of the skeletal remains that were associated with early human inhabitants before the great extinctions about 11,000 years ago. And among these sites most direct evidence of animals that were hunted and butchered consists of elephantlike proboscideans. Different proboscideans were available in different regions of the New World, and it is now evident that human hunting bands were able to adapt to each new species they encountered as they spread through the New World. The first humans to cross the Bering land bridge from Asia relied heavily on the woolly mammoth (*Mammuthus primigenius*) not only for food but also for much of their economy (including fuel, clothing, and shelter). When they reached approximately 50 degrees north latitude (near the present United States/Canada border), they encountered the Colombian mammoth (*Mammuthus columbi*) and despite its different appearance, behavior, and habitat preferences, this species was heavily hunted. It is the prey species most often associated with classic Clovis sites in temperate North America. In the eastern United States from Michigan to Florida, the American mastodon (*Mammut americanum*) was also frequently utilized by Paleoindians. In Central America and



4–7. *Cuvieronius,* scaled to a 2-meter human, belongs to a family of Mastodons called Gomphotheres that evolved from northern ancestors in the American tropics.

South America, however, a distinct family of proboscidea (Gomphotheriidae), most frequently Cuvier's gomphothere (*Cuvieronius tropicus*), formed the primary large-animal quarry for the earliest humans (fig. 4–7). A few sites scattered through the Americas yield more detailed evidence of how these various proboscidean species were butchered and utilized by the first Americans. The tusks were modified to elaborate ivory tools, including pointed foreshafts that were evidently attached to the fluted flint points and to the long spears or javelins that were used to hunt other proboscidea. Bones were often made into such tools as digging hoes, shaft straighteners, and hide burnishers. Much of this bone and ivory technology can be traced back to late Paleolithic traditions of Eurasia.

It is difficult to extend the argument for human hunting of the late Pleistocene megafauna beyond the proboscidea. Very rare evidence indicates occasional use of horses. Most of the other evidence implicates heavy hunting of buffalo in North America and llama in South America, but these are species that survive to the present. Thus the hypothesis that dozens of large-animal species were hunted rapidly to extinction during the late Pleistocene is very poorly supported by direct evidence.

On the other hand, the absence of evidence does not constitute evidence that human hunting did not occur. Perhaps most of the remains of horses and other large mammals were largely consumed, leaving limited evidence. Much more work is needed in very late Pleistocene sites that preserve large animal bones. It is certainly possible that the earliest Americans did heavily hunt the megafauna and contribute substantially to the extinction of dozens of species of megafauna. This view becomes difficult to deny when one imagines these early bands employing clever hunting strategies: blinds, decoys, trained dogs, and fire drives.

The American tropics somehow prevented the extinction of a number of megafaunal species that became extinct at higher latitudes both north and south. Many species of great ground sloths, for example, vanished throughout both continents, yet two genera and several species of tree sloths continue their sublime existence in the canopy, oblivious of the terrible fate of their many cousins. More impressive are the world's largest rodents, the capybaras, pursuing successful careers in wet tropical settings. Likewise, tapirs (see fig. 4–5C), spectacled bears (see fig. 4–5D), jaguars, and several kinds of llamas and peccaries represent a substantial variety of large mammals that are cited as human-caused extinctions in North America but seem to continue quite unmolested in tropical latitudes. Because the same kinds of human hunters who traversed temperate areas also traversed the tropics in the late Pleistocene, these examples support the climatic hypothesis. Evidently, late Pleistocene extinctions acted more severely at temperate latitudes, where the probable effects were extremes of rapid climatic change.

To summarize, one cannot understand Central America today without knowing its extraordinary prehistory and geologic history. Neither can one comprehend the natural history of South America without realizing how strikingly it was affected by the land bridge that connected it with the rest of tropical America and beyond. The resulting interchange about 2.4 million years ago saw an immense reciprocal rush of new groups moving through the isthmian link to occupy new terrain in another continent. Many families were involved, about half of them inhabitants of relatively open country (savanna) landscapes. And many groups more typical of temperate latitudes moved all the way through the American tropics.

In the second half of the Pleistocene, starting about 800,000 years ago, the isthmian landscape became more fully occupied by lowland rain forest. Late-arriving grazing animals such as buffalo and mammoth could not migrate south of the seasonally arid scrub forest along the Pacific slopes of Nicaragua. Instead, the land bridge supported a strong northward surge of tropical (Amazonian) land life that spread abundantly through Central America and north, especially along the moist Caribbean coast to about the tropic of Cancer in central Mexico. This still marks the northern limit of the Neotropical Biogeographic Realm.

About three dozen species of large mammals involved in the interchange suddenly went extinct about 11,000 years ago. The extinction episode took place more severely in temperate North America and temperate South America than in the tropics of Central America and northern South America, which hints at rapid climatic change at the end of the Pleistocene as the primary cause. On the other hand, another major impact on large mammals at that time was the rapid spread of hunting human tribes from Asia into the Americas. There is substantial direct evidence of their effect on such proboscidea as mammoths, mastodonts, and gomphotheres. It is much less clear how (or whether) they impacted other possible game animals that became extinct.

More than half of the present land mammals of South America came from North and Central America by way of the land bridge. That is a startling fact to many biologists, who would not have thought that such extensive change could take place in less than 3 million years throughout such a vast and varied continent. The fossil record makes it quite clear that these revolutionary events did take place on this rapid timescale. The vast opportunities created when new groups are suddenly able to enter new environments produce extraordinary evolutionary change and diversification. The interchange provides unique insights into those dramatic evolutionary processes that cannot be studied when species live under more stable conditions.

CHAPTER FIVE

The History of Forests on the Isthmus from the Ice Age to the Present

PAUL COLINVAUX

Over the past 2 million years the climate of the earth has changed repeatedly in sympathy with the advance and retreat of the great ice sheets of the north. Central America never experienced extensive ice coverage, except on the tops of the very highest mountains, for example, the Altos de Cuchumatanes in Guatemala and the Talamancas in Costa Rica. But so great a convulsion as an ice age must have been felt even far away from the ice sheets themselves.

The coastlines certainly changed as the level of the oceans fell. Subtract from the oceans water volumes big enough to cover Canada and Scandinavia with ice a mile or so thick and the sea shrinks by more than 100 meters. Geologists confirm that sea level dropped by finding the old shorelines under the modern oceans.

So the isthmus used to be broader, running out to what is now the fifty-fathom line, and there was more lowland. But what were those ancient lowlands like before the sea submerged them? To find out, scientists look for traces of ancient vegetation in the sediments of ancient lakes. These sediments may span a variety of time periods, but the most complete sequences record the history since the last major glaciation about 19,000 years ago. This chapter, then, focuses on the changes that took place during this last half of the glacial cycle. I want to look first at the way in which modern tropical pollen is identified and distributed and then at the changes in pollen composition through time as recorded in various lake cores.

Mud settles to the bottom of a lake every year, so that a lake 20,000