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## South Texas and the Great American Interchange

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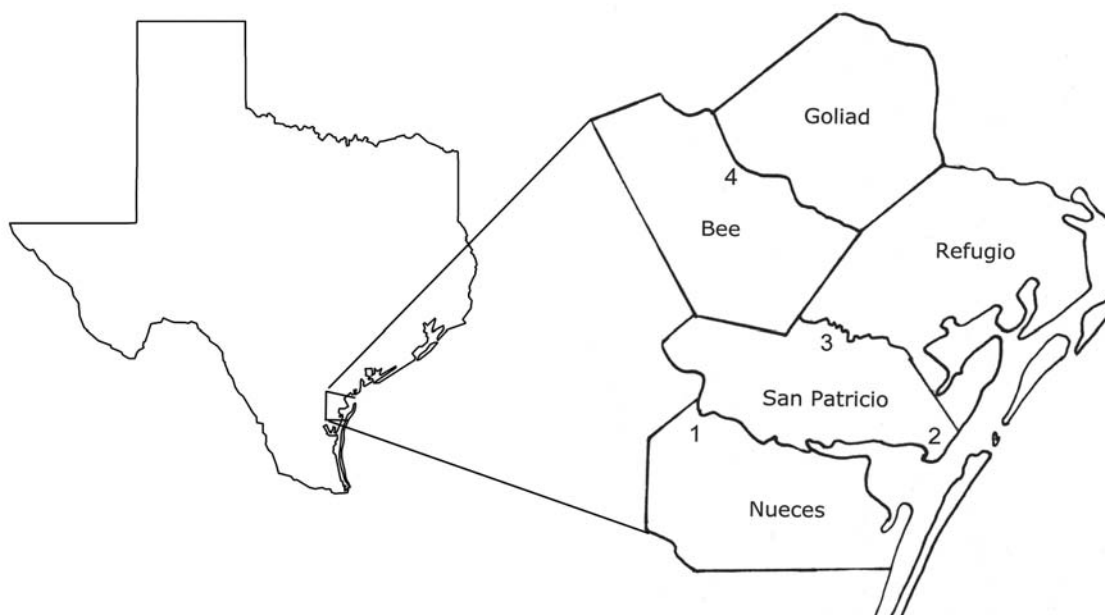
### ABSTRACT

South Texas has a rich late Cenozoic fossil record. At least 18 extinct genera and 27 extinct species of fossil mammals are known from the late Pleistocene alone. Many of these were participants in a major evolutionary event known as the Great American Biotic Interchange, which resulted from the formation of the Panamanian land bridge between North and South America. South American genera that traveled north and are present in the late Pleistocene of South Texas are the giant ground sloths *Ereotherium*, *Paramylodon*, and *Megalonyx*, the large relatives of armadillos *Holmesina* and *Glyptotherium*, and the capybara *Neochoerus*. North American genera that traveled south include the wolf *Canis*, the bears *Tremarctos* and *Arctodus*, the saber cat *Smilodon*, the gomphothere elephant *Cuvieronius*, the tapir *Tapirus*, the horse *Equus*, the peccary *Platygonus*, and the llamas *Palaeolama* and *Hemiauchenia*.

The 6.5 ft (2 m) tall, flightless, predatory, ‘terror bird’ *Titanis* is another South American immigrant. It had previously been thought that it entered North America about 2 Ma and survived in South Texas until the end of the Pleistocene. However, rare earth element dating of the South Texas *Titanis* shows that it arrived in North America in the early Pliocene (about 5 Ma), shortly before the completion of the Panamanian land bridge.

### INTRODUCTION

The Great American Biotic Interchange (GABI) was a major event in late Cenozoic biogeography as taxa from North and South America moved across the land bridge that formed with the emergence of the Isthmus of Panama (Simpson, 1950, 1980; Patterson and Pascual, 1968; Webb, 1976, 1985; Morgan, 2002, 2005). Situated on the coastal plain of the western Gulf of Mexico, South Texas (Fig. 1) was on the main highway of animals that migrated between the Americas. In the late Miocene and early Pliocene, 7 to 5 million years ago (Ma), before the land bridge was completed, a few land animals crossed the narrowed Panamanian seaway. These included two genera of giant ground sloths that traveled north and an extinct member of the raccoon family that traveled south. These have been termed “heralds” of the interchange (Webb, 1976). A notable addition to the herald taxa is the giant carnivorous ‘terror bird’ *Titanis* (MacFadden et al., 2007). During the late Pliocene and early Pleistocene, following completion of the Panamanian land bridge, representatives of 17 families of mammals migrated south and 10 migrated north (Webb, 2006). Many of these migrants have representatives in the late Pleistocene South Texas fossil record, which includes at least 18 extinct genera and 27 extinct species of Pleistocene mammals (Table 1).



**Figure 1. Locality map of South Texas Pleistocene sites discussed in this paper. 1 = Nueces River (this paper); 2 = Ingleside (Lundelius, 1972); 3 = Aransas River (Hay, 1926); 4 = Bee County (Sellards, 1940).**

## HISTORY OF FOSSIL VERTEBRATE COLLECTING IN SOUTH TEXAS

In natural history publications from the late 19th to mid 20th centuries, South Texas was usually referred to as “Southwestern Texas.” Perhaps the earliest description of a fossil from South Texas was by E. D. Cope, the foremost herpetologist and vertebrate paleontologist of his day. Cope (1880) noted the back end of a *Smilodon* (Pleistocene saber-toothed cat) skull collected from southwestern Texas by Gabriel Marnock, a pioneering Texas herpetologist who homesteaded near San Antonio (Stecker, 1933). In the late 1800s, Dr. William Taylor of San Diego, Texas, “a graduate of Edinburgh [Scotland], and a scholarly gentleman” (Bourke, 1894), made collections of Recent and fossil vertebrates that he sent to specialists for identification. Cope (1885, 1891) described much of this material, including the vertebrate fossils. Cope (1889) listed a mammoth, glyptodont, canid, and turtle and five species of horses from the “*Equus* beds” of southwestern Texas in what was then part of Nueces County. Gidley (1901) named a new species of horse *Equus giganteus* for the largest tooth in the collection. Dumble (1903) gave the locality as Taranchua Creek, a branch of San Diego Creek, near San Diego, Duval County, approximately 50 mi west of Corpus Christi. Sellards (1940) cited documentation justifying this locality assignment. Additional specimens of *Equus* from the San Diego area are in the collections of the Texas Memorial Museum (TMM).

Dumble (1903) reported on scattered mammal fossils from the Goliad Formation (Wilson, 1956). More extensive collections were made in Bee and Goliad counties by Works Progress Administration (WPA) crews of the Bureau of Economic Geology in the 1930s. Although it was initially assigned to the Pliocene, the now well-known mammalian fossils of the Goliad indicate a late Miocene age, about 11 Ma (Tedford et al., 1987).

Hay (1926) described a collection of 13 species of Pleistocene mammals made by Dr. Mark Francis, the first veterinarian at Texas A&M University, from the banks of the Aransas River, west of Sinton, San Patricio County. The late Pleistocene Berclair terrace of Blanco and Medio creeks, approximately 60 mi north northwest of Corpus Christi, in Bee and Goliad counties, has produced an assemblage of at least 18 species of mammals (Sellards, 1940; Quinn, 1957; Conkin and Conkin, 1962). By far the most important Pleistocene fossil locality in South Texas has been the Ingleside local fauna in San Patricio County on the north side of Corpus Christi Bay. The fossils were collected by WPA from 1939-1941. Lundelius (1972) described 31 species of fossil mammals from

Ingleside. Otvos and Howat (1996) determined that the pond containing the Ingleside fauna was mid to late Wisconsinian in age, postdating the Ingleside sands.

Four alluvial terrace units and three younger valley fill units are recognized from late Pleistocene and Holocene sediments in the lower Nueces River Valley, Nueces and San Patricio counties, west of Corpus Christi, Texas, between Odem and Mathis, where the Nueces River is entrenched in the late Pleistocene Beaumont Formation (Cornish and Baskin, 1995). Sand and gravel quarries from the valley fill and the youngest terrace have produced a reworked early Pliocene and an in-place late Pleistocene fauna (Baskin, 1991; Baskin and Mosqueda, 2002). Conkin et al. (1962) were the first to briefly note the occurrence of vertebrate fossils from one of these localities. The Wright Materials, Inc. quarries (TMM localities 43059 and 43064) are approximately 3 mi north of Bluntzer, Texas. A log from the valley fill which contains the in-place Pleistocene fauna has been dated at  $13,230 \pm 110$  BP (Baskin, 1991). Durbin et al. (1997) used thermoluminescence to date these deposits at 30-35,000 BP. Although few of the Wright quarry fossils are as complete as those from Ingleside, what is lacking in quality, they more than make up in quantity. For example, at Ingleside two mammoth mandibles and 12 isolated molars are present. McDaniel and Jefferson (2006) report on an older collection of 149 mammoth molars, which they mistakenly attribute to a gravel quarry near Mathis, San Patricio County, Texas. Over 170 complete horse metapodials and 29 radii are known from the Wright quarries compared to no horse metapodials and three horse radii from Ingleside.

## PLEISTOCENE INTERCHANGE MAMMALS FROM SOUTH TEXAS

### The South American Component

#### Xenarthra

The xenarthrans, also known as edentates, include the sloths, anteaters, and armadillos. There are two living genera of sloths, both relatively small and spending most of their lives hanging upside down from trees. Extinct sloths included large ground-dwellers. Mylodont and megalonychid sloths entered North America by 8 Ma (Marshall et al., 1979), before the completion of the Panamanian land bridge. Two of their relatives, *Paramylodon harlani* and *Megalonyx jeffersonii*, both of which occur across North America, are well represented in South Texas. *Paramylodon harlani* was a large grazer/intermediate feeder that weighed 1.5 tons (McDonald, 2005). *Megalonyx jeffersonii* was a low browser with a body mass of 1 ton (McDonald, 2005). This species is associated with forest and woodland habitats. The genus was named in 1796 by our third president Thomas Jefferson who thought its “great claw” (megalo-onyx) indicated the fossil was from a giant lion.

The megatheres include the largest of all the ground sloths. They first appear in North America in the late Pliocene (Morgan, 2005). *Eremotherium laurillardi*, which ranged from Brazil to South Carolina, was the size of a small elephant, with adult males over 20 ft (6 m) long and weighing more than 3 tons. This species is poorly represented in South Texas, being known only from two or three specimens from the Aransas and Nueces rivers.

*Holmesina septentrionalis* was a six foot long pampathere, a family of herbivorous armadillo-like mammals. James (1957) described a nearly complete specimen from Houston, as well as the material from Ingleside. The grazing glyptodonts include even larger shelled xenarthrans, with *Glyptotherium floridanum* weighing 1200 lbs (McDonald, 2005).

#### Rodents

Capybaras, the largest living rodents, are found in South and Central America. In the Pleistocene, they extended their range, from Arizona to Florida to South Carolina. The extinct *Neochoerus pinckneyi* weighed about 150 lbs, 40% greater than in living capybaras. Hay (1926) named this genus for material from the Aransas River, which he decided belonged to a species from South Carolina which he had assigned to the extant genus *Hydrochoerus*. Sanders (2002) determined that the species holotype from South Carolina was from 3 Ma, significantly older than the genotype locality in South Texas.

**Table 1. Faunal list of South Texas Pleistocene mammals. 1 = Nueces River (this paper); 2 = Ingleside (Lundelius, 1972); 3 = Aransas River (Hay, 1926); 4 = Bee County (Sellards, 1940). Presence is indicated by “+”, questionably present by “?”, and absence by “-”.**

	1	2	3	4
Order XENARTHRA				
Family Megatheriidae				
<i>Eremotherium laurillardi</i>	?	-	+	-
Family Mylodontidae				
<i>Paramylodon harlani</i>	+	+	-	-
Family Megalonychidae				
<i>Megalonyx jeffersonii</i>	+	+	-	-
Family Pampatheriidae				
<i>Holmesina septrionalis</i>	+	+	+	+
Family Glyptodontidae				
<i>Glyptotherium floridanum</i>	+	+	+	+
Order CARNIVORA				
Family Canidae				
<i>Canis dirus</i>	-	+	+	+
<i>Canis cf. lupus</i>	+	-	-	-
<i>Canis latrans</i>	-	+	-	-
Family Mustelidae				
<i>Mephitis mephitis</i>	-	+	-	-
Family Ursidae				
<i>Tremarctos floridanus</i>	+	+	-	-
<i>Arctodus simus</i>	+	-	-	-
Family Felidae				
<i>Smilodon fatalis</i>	+	+	-	+
<i>Panthera leo atrox</i>	+	+	-	-
<i>Puma concolor</i>	+	?	-	-
<i>Lynx rufus</i>	-	+	-	-
Order RODENTIA				
Family Sciuridae				
<i>Cynomys ludovicianus</i>	+	+	-	-
Family Geomyidae				
<i>Geomys</i> sp.	-	+	-	-
Family Hydrochoeridae				
<i>Nechoerus pinckneyi</i>	-	-	+	-
Order PROBOSCIDEA				
Family Mammutidae				
<i>Mammut americanum</i>	+	+	+	-
Family Gomphotheriidae				
<i>Cuvieronius</i> sp.	+	+	+	-
Family Elephantidae				
<i>Mammuthus columbi</i>	+	+	+	+

**Table 1 (Cont'd). Faunal list of South Texas Pleistocene mammals. 1 = Nueces River (this paper); 2 = Ingleside (Lundelius, 1972); 3 = Aransas River (Hay, 1926); 4 = Bee County (Sellards, 1940). Presence is indicated by “+”, questionably present by “?”, and absence by “-”.**

Order ARTIODACTYLA				
Family Tayassuidae				
<i>Platygonus compressus</i>	+	+	-	+
Family Camelidae				
<i>Camelops hesternus</i>	+	-	-	-
<i>Camelops</i> sp.	-	+	+	+
<i>Palaeolama mirifica</i>	+	+	+	-
<i>Hemiauchenia macrocephala</i>	+	-	-	?
Family Cervidae				
<i>Odocoileus virginianus</i>	+	+	-	+
Family Antilocapridae				
<i>Capromeryx furcifer</i>	+	+	-	-
<i>Tetrameryx shuleri</i>	+	+	-	-
<i>Stockoceras onusrosagris</i>	?	-	-	-
Family Bovidae				
<i>Bison latifrons</i>	+	-	-	+
<i>Bison antiquus</i>	+	+	-	-
<i>Bison</i> sp.	?	-	+	+
Order PERISSODACTYLA				
Family Tapiridae				
<i>Tapirus veroensis</i>	+	+	?	-
Family Equidae				
<i>Equus</i> spp.				

## The North American Component

### Carnivora

There were no placental mammal carnivores (Order Carnivora) in South America until about 8 Ma, when raccoon relatives dispersed over the narrow waterway separating the continents. The main invasion of placental carnivores began in the late Pliocene, when members of the dog, cat, and bear families crossed the land bridge. Until then marsupials, filled the canid and felid niches, even including a saber-cat-like marsupial. Tremarctine bears appeared in North America 7 Ma. *Tremarctos floridanus* is known from the late Pliocene and Pleistocene. It is best known from the late Pleistocene of the southeastern United States. The living South American spectacled bear *Tremarctos ornatus* does not have a fossil record. The short-faced bears *Arctodus*, from the late Pliocene and Pleistocene of North America, and *Arctotherium*, from the Pleistocene of South America, have been considered congeneric. In any event, *Arctodus* is ancestral to *Arctotherium*. The long-limbed *Arctodus* was the largest carnivore in the North American Pleistocene. The dire wolf *Canis dirus*, American lion *Panthera atrox*, and saber-toothed cat *Smilodon fatalis* were among the last participants of the GABI, appearing in Ecuador in the late Pleistocene (Kurtén and Werdelin, 1990). Lions entered North America from Eurasia in the late Pleistocene. The American lion, which is known from Alaska to Peru, was about 25% larger than the African lion *Panthera leo*. It is sometimes considered a subspecies, *Panthera leo atrox*. Although Pleistocene jaguars (*Panthera onca*) are known from Central Texas to California to Missouri to Florida in the late Pleistocene, none have been recovered yet from South Texas. A larger, exclusively South American saber-cat, *Smilodon populator* appeared in the middle Pleistocene. Both it and *Smilodon fatalis* are descended from the late Pliocene North American *Smilodon gracilis*.

## Artiodactyls

*Platygonus compressus*, the flat-headed peccary, was larger than its living relatives, such as the collared peccary (*Pecari tajacu*). *Platygonus* known from the late Miocene to the late Pleistocene in North America and first appeared in the South America in the early Pleistocene. Camelids initially evolved in North America in the late Eocene. In the Pleistocene they emigrated to Asia and Africa (camels) and to South America (llamas) and went extinct in North America. *Palaeolama* is ancestral to the South American guanaco (from which llamas and alpacas were domesticated) and vicuña. The slender, long-limbed llama *Hemiauchenia* migrated to South America in the early Pleistocene. New World deer include five South American genera that are most closely related to North American *Odocoileus* (white-tailed and mule deer). Deer are first known in South America in the middle Pleistocene.

## Perissodactyls

At least three species of *Equus* (which includes horses, zebras, asses) are present in South Texas in the late Pleistocene (Baskin and Mosqueda, 2002) and are perhaps the most common fossil present. *Equus* evolved in North America and then dispersed to the Old World 2.5 Ma and to South America 1.5 Ma. *Equus* became extinct in the New World 10,000 years ago, but was reintroduced by 1550, when domestic horses brought by the Spanish escaped and became feral.

Tapirs are primitive browsers that occur today in the tropical and subtropical forests of South and Central America (as well as Southeast Asia). Tapirs appear in South America 2 Ma, after emigrating from North America during the Pleistocene. They are poorly represented in South Texas. The late Pleistocene North American tapir is *Tapirus veroensis*.

## Proboscideans

Three families of elephants are present in North America during the Pleistocene. Mammoths are closely related to the living elephants, and entered North America from Eurasia in the Pleistocene. Mastodonts arrived in North America in the middle Miocene. Gomphotheres were mixed feeders (browsing and grazing); mastodonts, browsers; and mammoths and living elephants, grazers. Only the gomphotheres crossed the land bridge into South America. *Cuvieronius* arrived in South America in the early Pleistocene.

## PLIOCENE VERTEBRATES FROM SOUTH TEXAS

The South American immigrant taxa discussed above had their ancestors arrive in North America at least 2 Ma, long before these late Pleistocene fossil localities were formed. Baskin (1991) described latest Hemphillian (early Pliocene, about 5 Ma) horses from the Nueces River gravel pits. These horses are reworked from older deposits, presumed to be the upper Goliad Formation. The nearest exposures of the Goliad are approximately 10 km upriver from the sand and gravel pits near Bluntzer, Texas and 25 km from a gravel pit near Odem. Late Hemphillian horses from the gravel pits are *Dinohippus mexicanus*, *Astrohippus stockii*, *Nannippus* cf. *beckensis*, *Nannippus aztecus*, *Pseudhipparion simpsoni*, and *Neohipparion eurystyle*. Other evidence of an early Pliocene age for the reworked specimens are rhinoceros tooth fragments and parts of an edentulous *Rhynchotherium* mandible and palate. *Rhynchotherium* is a four-tusked gomphothere known from the late Clarendonian (late Miocene) through the late Blancan (late Pliocene). *Rhynchotherium* is ancestral to *Cuvieronius* and *Stegomastodon*, the two South American Pleistocene elephants.

The terror bird *Titanis* is also part of this reworked, early Pliocene fauna. *Titanis walleri* was a 6.5 ft (2 m) tall, cursorial, flightless, predator. It is distantly related to cranes. A Pliocene immigrant from South America, *Titanis* is fairly well known from the late Pliocene (about 2 Ma) of Florida (Gould and Quitmyer, 2005). *Titanis* from Texas is known from a single proximal phalanx from the gravel pit near Odem. Baskin (1995) considered that it might be late Pleistocene in age, since there is no evidence of two million year old mammals in the Nueces

River fauna and five million years is well before the main pulse of faunal interchange between the Americas. However, rare earth element dating shows that the Texas *Titanis* is the same age as the latest Hemphillian horses (MacFadden and others, 2007). *Titanis* therefore joins the list of Hemphillian heralds of the GABI.

## PLEISTOCENE MEGAFUNA AND HUMANS

The extinction of large animals (the megafauna) in North America at the end of the Pleistocene has been related to climatic changes and human influences (for a recent summary see Koch and Barnosky, 2006). Of the 26 genera of large mammals known from the Pleistocene of South Texas (Table 1), only the white-tailed deer (*Odocoileus virginianus*) and mountain lion still occur in the region. The extinction coincides with the arrival of the Clovis people in North America, circa 13,000 years ago, at about the time the valley-fill deposits of the Nueces River Valley were deposited. Clovis points are known from San Patricio County, although not in association with Pleistocene mammals (Chandler, 1982), and the Berclair Terrace (Sellards, 1940). A distal tusk and a long-bone section from the Nueces River gravel pits may have been modified by humans (Mandryk et al., 2005).

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## NOTES

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