LATE TERTIARY TERRESTRIAL MAMMALS FROM CENTRAL MEXICO AND THEIR RELATIONSHIP TO SOUTH AMERICAN IMMIGRANTS

OSCAR CARRANZA CASTAÑEDA

Unidad de Ciencias de La Tierra, Universidad Nacional Autónoma de Mexico, Campus Juriquilla, Querétaro, 76230, México. *carranza@geociencias.unam.mx*

WADE E. MILLER

Department of Geology, Brigham Young University, Provo, Utah 84602, USA. *wem@geology.byu.edu*

RESUMO - Nos últimos 25 anos ocorreram inúmeras descobertas de mamíferos neoterciários na região central do México, sendo que muitas vêm das bacias localizadas na Faixa Vulcânica Transmexicana. Em contraste com a maioria dos registros anteriores, estes achados têm sido cuidadosamente inseridos num contexto estratigráfico. Datações radiométricas em camadas de cinzas vulcânicas, juntamente com estudos paleomagnéticos, permitem o posicionamento do limite das Idades Mamíferos Terrestres da América do Norte *Hemphillian – Blancan* em 4,8 Ma. As pesquisas sobre os mamíferos neoterciários da região central do México também têm fornecido valiosas informações sobre novos táxons, ampliação da distribuição geográfica de muitos animais e mudanças ambientais na região. Vários mamíferos que imigraram da América do Sul durante o Neoterciário são também agora conhecidos na região central do México, adicionando novas e importantes informações concernentes à formação da ponte terrestre do Panamá e do Grande Intercâmbio Biótico Americano. Táxons como as preguiças *Megalonyx* e *Glossotherium*, os Cingulata *Glyptotherium* e *Plaina* e o roedor *Neochoerus* proveram dados relevantes a este evento. É geralmente aceito que a ponte terrestre do Panamá formou-se entre 2,5 e 3 milhões de anos atrás. Entretanto, as idades radiométricas e paleomagnéticas obtidas na região central do México associadas às informações aportadas pelos mamíferos imigrantes sul-americanos, indicam que esta ponte terrestre poderia ter-se originado mais de um milhão de anos antes. Por outro lado, o movimento tectônico, as mudanças de caráter insular e o vulcanismo na América Central durante o Neoterciário, com conseqüências eustáticas e na composição vegetal, tornam muito difícil a determinação cronológica precisa tanto da formação da ponte terrestre quanto do intercâmbio biótico resultante.

Palavras-chave: Hemphillian, Blancan, Faixa Vulcânica Transmexicana, Grande Intercâmbio Biótico Americano.

ABSTRACT – Many new discoveries of late Tertiary mammals have been made across central Mexico in the past two and one-half decades. Most came from basins located in the Transmexican Volcanic Belt. Unlike a majority of earlier finds, these have been carefully placed in a stratigraphic context. Associated volcanic ash layers have permitted a number of radiometric ages and, coupled with recent paleomagnetic studies, allow placement of the Hemphillian – Blancan North American Land Mammal Age boundary at 4.8 Ma. Research on late Tertiary mammals from central Mexico has also provided valuable information on new taxa, significant geographic range extensions for many animals, and environmental changes. Several South American immigrant mammals of late Tertiary age are now known from central Mexico. They add important new information concerning formation of the Panamanian land bridge and the Great American Biotic Interchange. Taxa providing relevant data regarding this event are the ground sloths *Megalonyx* and *Glossotherium*, the glyptodont *Glyptotherium*, the pampathere *Plaina,* and the capybara *Neochoerus*. It has been generally accepted that the Panamanian land bridge formed between two and one-half and three million years ago. However, radiometric and paleomagnetic age determinations in central Mexico associated with South American immigrants, indicate that this land bridge might have originated more than one million years earlier. Active plate movement in Middle America during the late Tertiary with attendant volcanism and insular changes, coupled with concurrent eustatic and vegetational changes, make chronologic precision regarding isthmus formation and the resultant biotic interchange difficult at best.

Key words: Hemphillian, Blancan, Transmexican Volcanic Belt, Great American Biotic Interchange.

INTRODUCTION

As used in this paper, central Mexico is that part of the country that lies between 19° and 23° North Latitude, excluding the northern portion of the tropical Yucatan peninsula. The southern extension of the Baja peninsula is included in this zone as it was situated within it during the late Tertiary according to Smith (1991). Almost all terrestrial vertebrates from the late Tertiary of central Mexico have been recovered from the states of Baja California Sur, Jalisco, Zacatecas, Michoacán, Guanajuato, Querétaro, San Luis Potosí, México, Tlaxcala, and Hidalgo (Figure 1). Additional states or portions of them also lie within the above latitudinal zone. However, they mostly have not yet been intensively searched for fossils. The state of Aguascalientes, though, has yielded both pre-Hemphillian Miocene mammals (Dalquest & Mooser, 1974) and locally abundant Pleistocene vertebrates (Mooser & Dalquest, 1975; Dalquest & Mooser, 1980). In the case of the state of Veracruz, abundant vegetation seriously limits effective searching for fossils. It should be noted, however, that a very small Pleistocene vertebrate fauna was reported from Veracruz by Dalquest (1961). This consisted of limited material representing three mammalian genera and a few unidentified bird bones. In the case of the Yucatan peninsula, we are not aware of any late Tertiary terrestrial vertebrates from the states of this region.

The late Tertiary as defined here constitutes the Hemphillian and Blancan North American Land Mammal Ages (NALMA). Lindsay (2001) placed the base of the Hemphillian at about 9.4 Ma and the top of the Blancan at about 1.8 Ma. While he also (Lindsay *et al.,* 2002) placed the Hemphillian-Blancan boundary at about 4.9-5.0 Ma based on paleomagnetic and radioisotopic dating of strata in Nevada, our work in central Mexico (Kowallis, *et al.*, 1998) has shown that this same boundary exists here at approximately 4.8 Ma. Our additional paleomagnetic and radioisotopic dating in central Mexico further substantiates this boundary placement (Flynn

et al., in press). Earlier research produced a later boundary date yet. It was given as, "probably between 4.0 and 4.4 Ma" by Lundelius *et al.*, 1987).

Extensive fossiliferous exposures of late Tertiary sediments in central Mexico represent the southernmost ones on the North American continent. These are dominated by late Hemphillian and Blancan age strata. During the earliest Blancan the Great American Biotic Interchange (GABI) between North and South America was undergoing its initial stages. It is in central Mexico that the first mammalian immigrants of this interchange are found. And although earlier South American mammals have been discovered in northeastern Mexico (McDonald, pers. comm.) and in the southern tier of states in the United States (e.g., Hirschfeld & Webb, 1968; Marshall, 1985; Wagner, 1981), they appear to have immigrated before the formation of the Panamanian land bridge. The GABI, as presently understood, postdated these first mammalian immigrants, and appears to have begun at about the Hemphillian – Blancan boundary.

Until relatively recently, late Tertiary vertebrates from Middle America have been poorly known. The best record to date comes from recent work in central Mexico (Carranza, 1989; Carranza *et al.*, 1994; Miller, 1980; Miller & Carranza, 1984, 2001). This record forms the main basis for the present analysis. Only minimal paleontological research was conducted in Mexico prior to the mid-to-late 1970's. What was previously done generally provided little or no stratigraphic context with collected fossils specimens (e.g., Dalquest & Mooser, 1980; Freudenberg, 1910, 1922; Leidy, 1882; Mooser, 1964, 1973). Research on Hemphillian and Blancan age vertebrates in central Mexico in the past 15 years has provided a stratigraphic context with collected specimens, as well as radiometric and paleomagnetic age determinations of faunas (Figure 2). Some of these dates pertain to South American immigrants (Carranza *et al.*, 2000; Flynn *et al.*, in press; Kowallis *et al.*, 1986, 1998).

GEOLOGIC SETTING

Excluding the Yucatán peninsula and the state of Veracruz, most of central Mexico falls within the Sonoran Desert province. As such it currently receives sparse rainfall. In the state of Guanajuato for example, the average annual rainfall is about 50 cm per year. It is the low annual precipitation in most of central Mexico that is responsible for large areas of exposed fossiliferous sediments.

Most of central Mexico is largely dominated by volcanic uplands which constitute the Transmexican Volcanic Belt (TVB, Figure 3), and two prominent mountain ranges. The Sierra Madre Oriental runs along the eastern part of Mexico, while the Sierra Madre Occidental runs along the west. Both ranges trend roughly northwest-southeast. It has been stated that the Sierra Madre Occidental represents, "the largest continuous expanse of silicic ignimbrites in the world" (Aguirre-Díaz *et al*., 1997). The TVB runs essentially east-west from coast to coast between latitudes 19° and 21° North. Magmatism responsible for volcanic activity in early to middle

Figure 1. Index map showing major areas where late Tertiary fossil vertebrate localities have been discovered and developed during the past 25 years in central Mexico (BCS = Baja California Sur; CHI. = Chihuahua; ZAC. = Zacatecas; JAL. = Jalisco; GTO. = Guanajuato; HGO. = Hidalgo; MICH. = Michoacàn; MEX. = México; TLAX. = Tlaxcala).

Miocene time is thought to be due to subduction of the Cocos and Rivera plates along the Middle America Trench (Aguirre-Díaz *et al.*, 1997). Our fieldwork in central Mexico, along with that of others, shows the volcanic rocks to be largely rhyolites and basalts. The time of initiation of volcanic activity that produced the TVB is still unclear. Cited ages range from the late Oligocene to the middle Miocene (Ferrari *et al.*, 1994). The oldest extensive fossil-bearing sediments thus far discovered within this Belt are late Miocene (Hemphillian) in age.

North to northwest trending normal faults cutting across the Transmexican Volcanic Belt, presumably originating in the Miocene (Aguirre-Díaz *et al.*, 1997), produced a series of horsts and grabens. This appears to be the southernmost extension of the Basin and Range province (Henry, 1989; Kowallis *et al.*, 1998). These grabens constitute elongate basins that are mostly oriented roughly north-south. An overwhelming majority of vertebrate fossils from central Mexico have been recovered from these basins that extend from the state of Hidalgo on the east, westward through southern Baja California Sur (Carranza & Miller, 1999). With the exception of southernmost Baja, which does not contain latest Tertiary volcanic rocks or ashes (Martínez & Sethi, 1997), these basins are bounded by volcanic uplands. As a result, volcaniclastic rocks make up the bulk of fossil-bearing sediments. Most are alluvial and fluvial, with some being lacustrine. Floodplain deposits seem to predominate. Volcanic ash layers are intercalated within these central Mexican sedimentary basinal deposits, except in southernmost Baja California. Many of these ashes have been dated; others are still in the process of age determination. In some instances vertebrate fossils have been recovered from these ash layers. Our work on dating these ashes and on volcanic rocks from several of the basins has produced late Tertiary ages ranging from about 31-22 Ma for the volcanic rocks and 9-3 Ma for the ashes. Other work (Aguirre-Diaz, pers. comm.) has shown that the most intensive period of volcanic activity throughout the TVB (Figure 3), but especially in the central and western portions of it, occurred between about 8–12 Ma. This activity continued from about 8-5 Ma., but to a lesser degree in the region. This continuous volcanic activity seems to explain the paucity of sedimentary deposits prior to the late Hemphillian in the affected area. And with this paucity of sediments, there is a concomitant scarcity of earlier age Miocene terrestrial fossils. Some volcanic activity persisted in the region, much of which is attested to by widespread volcanic ashes during the late Hemphillian and Blancan. It is these ashes that have made radiometric datings of the faunas possible.

DISCUSSION

General discussion of the Central Mexican fauna

In 1984 Miller & Carranza revised the state of late Cenozoic vertebrate paleontology in central Mexico up until that time, and showed that very few researchers had provided significant stratigraphic data for fossil localities. Also, no radiometric or paleomagnetic ages had then been determined
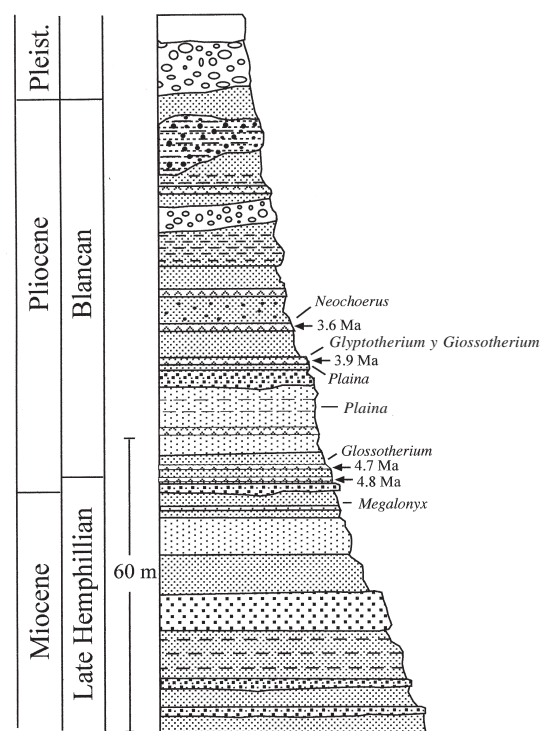

Figure 2. Composite stratigraphic section of sediments in the San Miguel Allende Basin, Guanajuato, Mexico, showing earliest radiometric ages for South American immigrants.

for any late Tertiary faunas. Most published radiometric age dates pertaining to vertebrate fossils in Mexico concerned the late Pleistocene (e.g., Alvarez, 1969). Aside from our work on the late Tertiary, radiometric dates in Mexico still mostly relate to the Pleistocene (e.g., Pichardo, 1997, 1999, 2001). Beginning in the mid-1970's, the Instituto de Geología at the Universidad Nacional Autónoma de México in Mexico City initiated a paleontological and geological project. The intent was to provide detailed coordinated paleontologic and geologic data. This effort marked the first serious attempt to provide detailed chronobiostratigraphic studies for central Mexico and beyond. It continues to the present.

The most intensive fieldwork since the mid-1970's has been done in the state of Guanajuato, followed by the states of Jalisco, Hidalgo and Baja California Sur. Other investigated states, as mentioned above, have yielded important fossil localities but they have not yet been as comprehensively studied (Carranza & Miller, 1997; Miller & Carranza, 2001). Table 1 shows both Hemphillian and Blancan age fossils identified for each central Mexican state in which they were collected. Within the state of Guanajuato the San Miguel Allende basin, with its extensive fossil-bearing sediments of Hemphillian and Blancan age, has served as a standard to which other fossiliferous deposits from other central Mexican areas have been compared. The most extensive faunas to date come from this basin. This basin's geology has also been much more intensively studied in conjunction with late Tertiary fossils than in any comparable age terrestrial

vertebrate-bearing deposits in all Mexico (Adams, 2001; Carranza *et at*., 1994; Carranza & Miller, 2000; Kowallis *et al*., 1998). Because sediments in the San Miguel Allende basin contain volcanic ash units at various intervals throughout the stratigraphic sequence, it has been possible to obtain precise ages for included faunas. This holds true for both deposits of Hemphillian and Blancan age. Additionally, some volcanic basement rocks in the basin were also radiometrically dated. To obtain the radiometric ages on these basinal deposits both single-crystal ^{40}Ar/ ^{39}Ar laser-fusion and fission-track methods have been used. Results of these radiometric analyses can be found in Kowallis *et al*. (1986, 1998). In the mid-1990's sampling of Hemphillian and Blancan sediments was begun in the San Miguel Allende basin for the purpose of obtaining paleomagnetically derived ages. Results of this work will soon be published (Flynn *et al*., in press). Paleomagnetic samples will next be collected in fossiliferous deposits of the Tecolotlan basin of Jalisco early in 2003. Some radiometric dates have been obtained from fossiliferous deposits in the states of Jalisco and Hidalgo (Kowallis *et al*., 1998). More are planned. Field work has taken place regarding late Cenozoic terrestrial vertebrate paleontology and geology in southernmost Baja California Sur for many years (Carranza & Miller, 1999; Miller, 1977, 1980; Miller & Carranza, 2002; Torres, 1980). Reasonably abundant terrestrial vertebrate fossils of early Blancan age have been recovered, but none certainly of Hemphillian age. To date, no South American immigrants of Blancan age have been discovered here. This might be explained by the separation of Baja California from the Mexican mainland at this time. Also, no associated volcanic ashes have been located. The southernmost part of the Baja peninsula has had a separate geologic history from the main portion of the peninsula, and is known as the Los Cabos block. The youngest volcanic rocks and sediments pertaining to this block appear to be no younger than early Miocene (Fierstine *et al*., 2001; Helenes & Carreño, 1999; Martínez & Sethi, 1997). However, middle Miocene volcanics do occur immediately to the north (Helenes & Carreño, 1999). Magnetostratigraphy

Figure 3. Map of Mexico showing the generalized area of the Transmexican Volcanic Belt.

in the fossil-bearing sediments of the San José del Cabo basin of southernmost Baja is planned by the present authors. This is especially important due to a lack of volcanic ash in the area. Both radiometric and paleomagnetic age datings are projected for fossiliferous beds in other central Mexican states in the near future.

Faunal constituents and ages

During the past 25 years intensive field work in central Mexico has resulted in the discovery and collection of several thousand Hemphillian and Blancan age terrestrial vertebrate fossils. Almost all have been collected in a stratigraphic context. For the most part these have all been cataloged and are currently housed with the paleontological collections at the Instituto de Geología, Universidad Nacional Autónoma de México (UNAM) located in Mexico City. And, as mentioned above, many datable volcanic ash layers as well as paleomagnetic datings have provided chronologic precisions for them. The many identified mammalian genera appear in Table 1, which gives an idea of how extensive the fossil data base is. This table indicates which NALMA is involved with each taxon in addition to the central Mexican state in which each was found. Chihuahua, although in northwestern Mexico, is also listed in the table. Its listing occurs because, aside from central Mexican faunas, it contains the most complete Hemphillian, and to a lesser extent Blancan, age terrestrial mammalian faunas from all Mexico. The late Hemphillian Yepómera fauna from Chihuahua had long been considered the most complete Mexican fauna of this age. The Hemphillian and Blancan age faunas from Guanajuato, though, now exceed those from Chihuahua in both numbers and diversity (see Table 1). Those from Guanajuato have been used as a standard to which others from central Mexico are compared.

A number of articles contain general discussions of the late Tertiary vertebrates from parts of central Mexico (e.g., Carranza, 1989; Carranza *et al*., 1994; Carranza & Miller, 2000; Miller & Carranza, 1984, 2001), while others contain discussions of specific taxa (e.g., Carranza & Espinosa, 1994; Carranza & Miller, 1988, 1996; Carranza & Walton, 1992; Miller & Carranza, 1982, 1996, 1998). It is therefore deemed unnecessary to further discuss these taxa with the exception of the South American immigrants. All late Tertiary vertebrates we have collected in central Mexico to date fall within either the Hemphillian or Blancan NALMA. None of the Hemphillian fossils thus far identified come from deposits of the early part of that age, however. As mentioned above, though, a very small pre-Hemphillian Miocene local fauna was described by Dalquest & Mooser (1974) from the central Mexican state of Aguascalientes. They indicated a Barstovian age for this the Zoyatal local fauna. Ferrusquia later (1990) assigned this local fauna to the medial Hemingfordian NALMA. Most likely some early Hemphillian fossil-bearing deposits as well as other pre-Hemphillian Miocene ones exist along the TVB. But these most certainly are rare, as fairly detailed searching in this region has thus far failed to identify any. As stated above, extensive volcanic activity throughout the Transmexican Volcanic Belt during this time probably limited

Table 1. Faunal list for Hemphillian (H) and Blancan (B) mammalian taxa from central Mexico and Chihuahua. State abbreviations: CHIH. = Chihuahua; S.L.P. = San Luis Potosí; JAL. = Jalisco; GTO. = Guanajuato; QRO. = Querétaro; HDO. = Hidalgo; MICH. = Michoacán; MEX. = México; TLAX. = Tlaxcala; B.C.S. = Baja California Sur. * = Type specimen from Mexico.

Taxa	CHIH	S.L.P.	JAL	GTO	QRO	HGO	MICH	MEX	TLAX	B.C.S.
Order Insectivora										
*Notiosorex *repenningi*	H			?H		?H				
Notiosorex sp.	B									
Order Chiroptera										
**Plionicterus* sp.*	H			?H		?H				
Order Edentata										
Glyptotherium sp.			B	B						
Plaina sp.				B						
Glossotherium sp.				H,B						
Megalonyx sp.			H	H		H				
Order Lagomorpha										
Archaeolagus sonoranus	H									
cf. *Sylvilagus hibbardi*	H									
Sylvilagus sp.							?B			
*Hypolagus *mexicanus*				B						
Hypolagus cf.. *H. vetus*										B
Hypolagus sp.			?H	H		?H				
Notolagus velox				H		H				
**Paranotolagus *complicates*										
Pratilepus ?kansasensis										
Order Rodentia										
Spermophilus pattersoni	H									
*Spermophilus *matachisensis*	H			?B						
Sphermophilus shotwelli	H									
Sphermophilus sp.	H			H, B		?H	?B			
*Ammosphermophilus *jeffriesi*										B
Paenemarmota barbouri	H			H, B			B			
Castor cf. *californicus*	H									
Perognathus henryredfieldi	H									
Perognathus sp.	H									
Prodipodomys idahoensis	H									
*Pliogeomy *carranzai*	H									
?Pliogeomys sp.				H						
Geomys minor	B									
Copemys near C. valensis	H			?H						
*Calomys *elachys*	H, B			H						
*Calomys *baskini*	H, B			H						
*Calomys *winklerorum*				H						
Calomys sp.	H		?H							
Baiomys kolbi	H, B			H						
Prosigmodon oroscoi	H, B			H						
*Prosigmodon *chihuahuensis*	H, B			H						
*Prosigmodon *ferrusquiai*				H						
Neotoma cf. *N. sawrockensis*				H						
Neotoma sp.			?H	H		?B				B
Pliophenacomys sp.	B									
*Neochoerus *cordobai*			B	B						
Neochoerus sp.				B						

Table 1. (continuation)

Order Carnivora											
*Canis *ferox*			H	H		H					
Canid indet.	H, B										
Vulpes sp.	H										
*Cerdocyon *avius*											B
Osteoborus cyonoides			H	H							
Osteoborus cf.. *O. cyonoides*	H				H						
*Borophagus *matthewi*								B			
Borophagus diversidens				B							
Borophagus ?diversidens					B						B
Agriotherium schneideri	H			H							
Agriotherium cf. *A. schneideri*	H		H			H					
Tremarctos sp.						B					
*Taxidea *mexicana*	H										
cf. *Mustela*				H							
cf. *Trigonictis*				B							
Chasmoporthetes johnstoni	B										
Pseudaelurus ?intrepidus				H							
?Pseudaelurus sp.	H										
Felis cf. *F. studeri*				B							
Felis ?lacustris				?B							B
cf. *Machairodus* sp.											B
Nimravides catacopsis	H										
Order Proboscidea											
Gomphotherium sp.					H						
Stegomastodon sp.				H							
cf. *Stegomastodon*	H,B										
Cuvieronius sp.	H,B		?B	?B							
*Rhynchotherium *browni*	B										
*Rhynchotherium *tlascalae*									?H	?HB	
Rhynchotherium cf. *R. falconeri*				HB				B			B
Rhynchotherioum sp.			H			?H					
gomphotheriid indet.			H				?H				
Order Perissodactyla											
Teleoceras fossiger	H		H	H		?H					
Teleoceras sp.		?H				H	H				
*Calippus *castilli*			H	H			H				
Neohipparion eurystyle	H		H	H	H	H	H		?H		
Nannippus minor	H		H	H	H	H					
*Nannipus *peninsulatus*	B		B	B		B	B				
*Astrohippus *stockii*	H	H	H	H		H					
Dinohippus interpolatus			H	H	?H	H	H				
*Dinohippus *mexicanus*	H	H	H	H		H					
Equus cf. *E. simplicidens*			B	B		B	B				B
Order Artiodactyla											
Prosthennops sp.	H		H	H		H					
Platygonus sp.				B			B				
tayassuid indet.	H										
Megatylopus matthewi			H	H							
?Megatylopus sp.	H									?H	
Titanotylopus sp.	H										
Hemiauchenia sp.	H		?B	HB		H	B			?B	B
cf. *Camelops*				?B							B
camelid indet.			H			H	H				
Hexobelomerix fricki	H		H	H	H	H					
antolocaprid indet.			B								B

sedimentary deposits, and deeply buried those that did form. This would explain the rarity of pre-late Hemphillian and earlier Miocene terrestrial fossils across the region.

From the southern part of Mexico Ferrusquia (1990) described a very small vertebrate fauna, the Ixtapa local fauna, from the state of Chiapas. He indicated an age of late Clarendonian to early Hemphillian for it. It therefore appears that in all Mexico early to middle Hemphillian age deposits, which contain diagnostic fossils, are extremely rare to lacking based on present knowledge. This information bears considerably on the faunal interchange between North and South America, and will be discussed below.

Overview of the Great American Biotic Interchange (GABI)

Many researchers have discussed the biotic interchange (GABI), mostly regarding the mammals, between North and South America. Some of the earlier well considered concepts relating to this were expressed by Matthew in 1915 and later expanded by him in 1939. Subsequently, Simpson (1950, 1965) reviewed previous work on this topic and greatly added to it. More recent research concerning the GABI has been built upon the concepts of these two workers especially.

It has been long known, and essentially unanimously accepted, that South America was an island continent from the early through the late Tertiary, and that during the tens of millions of years it was an island continent, its biota evolved separately from other land masses. Differences of opinion, though, have arisen over the time of connection between North and South America and to the details of how this took place (Whitmore & Stewart, 1965). As stated by Coates (1997), "Not surprisingly, there is controversy concerning the timing and direction of the complex plate movements that led to the creation of the Central American land bridge." In addition to the tectonic and volcanic activity of plate movements that led to the creation of this land bridge, concurrent glacial build-ups and destructions in high latitudes undoubtedly complicated the picture. As early as in the Oligocene epoch cooler World-wide conditions brought on some glaciation. Warming and cooling conditions continued intermittently through time. By the latest Miocene a major expansion of the Antarctic ice sheet was underway (Dott & Prothero, 2002). Well known glacial and interglacial conditions marked the late Pliocene and the Pleistocene. Therefore, eustatic changes undoubtedly affected the developing isthmus. It seems reasonable to assume that connections and near connections of the pre-isthmus archipelago, and then conditions of the Central American isthmus itself, must have changed considerably from the late Miocene into the Pleistocene. Even at present the Pacific Ocean and Caribbean Sea might connect along the Nicaragua-Costa Rica border with a sea level rise. Coates (1997) indicated that the lowest relief of the Isthmus is just 45 m in this region. Melting of present ice sheets would accommodate a breaching. The dispersing of animals between the North and South American continents during the late Cenozoic would have been further complicated by changing vegetational zones (Alvarado, 1994; Colinvaux, 1997; Webb, 1997).

Simpson (1965), who popularized the concept of island-hopping, indicated that caviomorph rodents and monkeys reached South America from North America in this manner. Marshall (1985) stated that this dispersal happened during or just prior to Deseadan age Oligocene. However, he said that this waif dispersal to South America could have been from Africa rather than from North America. The dispersals in these instances must have been via vegetational rafting because of presumed relatively great distances of over-water travel. It is interesting to note that no South American emigrants have been identified anywhere in North America at this time. Apparently existing ocean currents were not conducive for this.

The earliest known late Tertiary exchanging of taxa between North and South America occurred in the Hemphillian. This undoubtedly represented a filter type of dispersal and probably involved island-hopping. Simpson (1965) stated that Middle America served as a faunal filter for the North American animals that reached South America. He further related that these emigrants did not come from the North American continent as a whole, but were ones adapted to conditions prevalent in Middle America at the time. Among the mammalian groups represented there by fossils in the Miocene were mastodonts, carnivores, rodents, rhinos, horses, peccaries, camels, protoceratids, and deer (Ferrusquia, 1984, 1990; Webb, 1997; Webb & Perrigo, 1984). Until recently only one of these groups was recognized in South America as early as the early Hemphillian. This immigrant, *Cyonasua*, belonging to the Carnivora family Procyonidae, has reasonably good representation in Argentina. Its presence there has been given by Webb (1976, 1997) as occurring about 8 Ma. Marshall (1985) dated various Argentinian finds from about 6 to 7.5 Ma. A newly found Miocene age immigrant to South America is the mastodont, *Amahuacatherium,* from Peru (Campbell *et al*., 2001). This gomphothere has been given a minimum age of 9 Ma based on ^{40}Ar/ ^{39}Ar dating of volcanic ash deposits and by magnetostratigraphy. This increases the earliest record of the Proboscidea in South America by several million years. Previously, Dudley (1996) implied that the first members of this order reached South America no earlier than the late Pliocene. Simpson & Paula Couto (1957) indicated that proboscideans in Brazil are unknown prior to the Pleistocene. Since gomphotheres were almost certainly too large to have immigrated to South America on vegetative rafts (although they may have traveled alongside them), they must have island-hopped by swimming. Elephants are strong swimmers. With a similar body build, it seems reasonable to assume that mastodonts were, too. Johnson (1978) indicated that mammoths reached the Channel Islands of California by swimming , and that modern elephants have been known to swim great distances. He indicated that olfactory sensing of insular food during times of drought or other vegetative diminution would provide motivation to swim to islands. Agenbroad (pers. comm.) stated that modern elephants have been known to swim distances in excess of 30 miles. Other animals apparently made water crossings between islands in the late Tertiary of Middle America as well. Alvarado (1994) noted that the crocodile, *Cha-*

ractosuchus, is known from both Americas in the Miocene, along with a colubrid snake.

The earliest certain late Tertiary mammalian immigrant in North America from South America is the megalonychid ground sloth, *Pliometanastes* from California and Florida (Hirschfeld, 1981; Marshall, 1985). A radiometric age based on a tuff overlying the California partial skeleton was given at a little more than 8 Ma. (Wagner,1981). *Thinobadistes*, a mylodontid ground sloth known from Florida and Texas (Webb, 1989), is roughly the same age (Marshall, 1985). Webb (1989) described two species of *Thinobadistes*, one from the early Hemphillian of Florida and the other from the medial Hemphillian of central Florida and from the Panhandle of Texas. To date this genus has not yet been recovered from Mexico. According to Hirschfeld (1981), the ground sloth *Megalonyx* first appeared in North America in the late Hemphillian as an immigrant from South America. Its earliest appearance seems to be from the Optima, Oklahoma local fauna (Hirschfeld & Webb, 1968). This fauna roughly correlates to the 5-6 Ma. Coffee Ranch local fauna of Texas (Tedford *et al.*, 1987). Another very early record of *Megalonyx* is *M. mathisi* from beds in California tentatively correlated with the Pinole Tuff, dated at 5.2 Ma. However, there are no authenticated records of this genus outside North America. Its furthest southern known occurrence is in the late Hemphillian of central Mexico. Considering the early arrival of *Pliometanastes* and *Thinobadistes* in North America, these genera must have immigrated there by a water route. Webb (1997) considered ground sloths to be durable swimmers and adapted to live in a wide variety of environments. Hirschfeld (1985) presented a good argument for sloths ability to island-hop. The recent discovery of a semiaquatic sloth in marine Pliocene deposits of Peru (Muizon & McDonald, 1995), further strengthens the concept that sloths possessed swimming abilities. Presence of megalonychids in several of the Greater Antilles' islands in the mid-Tertiary (Hirschfeld, 1985) indicates over water travel. Whether their movements were by swimming or by rafting (or both) remains unresolved. Hirschfeld (1985) believed that the Caribbean sloths represent a different dispersal route than those known from North America based on taxonomic differences.

Faunas from central Mexico give cause for a reappraisal of timing for the formation of the Panamanian land bridge. The classical view is that the first South American animals to walk across the Panamanian land bridge did so in the latest Pliocene, thus initiating the GABI. Dates given for the establishment of this overland passage usually are in the 2.5 to 3.1 million year range (e.g., Coates & Obando, 1996; Keigwin, 1978; Marshall, 1985; Webb, 1991). But as shown below, discoveries in central Mexico have altered this view, providing evidence for an earlier forming of the Isthmus. However, Cione and Tonni (1995, 1996, 1999) in discussing the timing for North American mammalian immigrants into South America stated that most records of North American families arriving in South America are younger than commonly given (i.e., less than 2.5 Ma). They did indicate, though, that South American "Land Mammal Ages" exist in a state of change regarding their concept, acceptable names to be used,

and age datings. It should be noted that some researchers working with marine invertebrates have suggested a Central American isthmus forming as early as the late Miocene (e.g., Kaneps, 1970; Parker, 1973; Woodring, 1966). Hoernle *et al.*, (2002) suggested that a Central American land bridge formed about 4.6 Ma. A possible reason for differing dates regarding the closing of the Central American seaway and forming of a Central American isthmus is that shallow breaches occurred at times during the Pliocene or even later. There have been recent suggestions that isthmus closure was not a single event (Coates & Obando, 1996).

Webb (1976) listed the mammalian taxa involved in the GABI. According to him (1997), those that walked across the Isthmus began this dispersal about 2.4 Ma. Marshall (1985) stated that the first great contingent of South American immigrants appeared in North America near the end of the Blancan at about 2.6 to 2.8 Ma. The "walking" immigrants included two ground sloths, *Eremotherium* (DeIullis & Cartelle, 1999) and *Glossotherium* (Robertson, 1976), armadillos, pampatheres, glyptodonts, capybaras, porcupines and a phorusrhacid bird. The peak of the interchange probably occurred sometime in the Irvingtonian NALMA, but continued into the Rancholabrean. According to Webb (1997), 35 families of mammals and one of bird were involved in the GABI. These are nearly evenly divided between North American and South American forms. 17 mammalian families dispersed from north to south, and 18 from south to north. Marshall (1985) listed 45 genera of mammalian dispersants from North America to South America, and 13 from South America to North America. *Megalonyx* is not one of the genera listed by him.

Relationship of the Central Mexican fauna to the Great American Biotic Interchange

Although many researchers have studied and discussed the method and timing of the formation of the Central American isthmus and the resultant biotic interchange, significant differences of opinion still exist as related above. Disciplines involved in the study include geology (Coates, 1997; Coates & Obando, 1996; Hoernle *et al.*, 2002; Woodring, 1966), invertebrate paleontology (Budd *et al.*, 1996; Jackson & D'Croz, 1997; Keigwin, 1978), Paleobotany (Colinvaux, 1996, 1997), vertebrate paleontology (Marshall, 1985; Simpson, 1950, 1965; Webb, 1976, 1997) and paleoecology (Webb, 1991). In 1997 Webb indicated early North American immigrants from South America in southern California and southern Arizona helped establish a 2.4 Ma forming of the Central American land bridge. He also said that immigrants from South America occur in late Pliocene sediments of Central America. However, he failed to mention that several reports of Pliocene South American immigrants had been made for central Mexico that predated both the United States and Central American records (e.g., Carranza, 1989; Carranza *et al.*, 1981, Carranza & Miller, 1980, Carranza & Miller, 1988; Miller & Carranza, 1984). Likewise Woodburne & Swisher (1995) did not include the central Mexican late Tertiary South American immigrants in their extensive paper on interconti-

nental overland dispersals of mammals. They further stated that stratigraphic sections which span the Hemphillian-Blancan boundary are rare. While they mentioned one from southern California, it was indicated that few Hemphillian fossils were present. Unfortunately, they overlooked reports of sections spanning this boundary in central Mexico where both Hemphillian and Blancan mammals occur in abundance (e.g., Carranza *et al.*, 1982; Carranza & Miller, 1989; Miller & Carranza 1984). It therefore becomes evident that more emphasis needs to be attached to the late Tertiary appearance of South American immigrants into central Mexico and to the excellent representation of sedimentary sections there, many with volcanic ash units included, spanning the Hemphillian-Blancan boundary. Vertebrate fossils exist in most of these sections, often in abundance. While the Hemphillian and Blancan age sedimentary sections have been studied more intensively in the state of Guanajuato, and most vertebrate collections made here, other fossiliferous sections containing South American immigrants of these ages occur in the states of Hidalgo and Jalisco. Recent field research has already led to identifications of fossils of late Tertiary age from other central Mexican states. This work will continue.

The earliest record of a South American immigrant in Mexico is the megalonychid, *Pliometanastes* from the northeastern state of Nuevo Leon. Although a nearly complete skeleton was collected through the California Institute of Technology in 1931, identification of it by Gregory McDonald was not made until recently (McDonald, pers. comm.). Wherever *Pliometanastes* has been recovered with an associated fauna, it has been designated as early Hemphillian in age. It is probable that the Nuevo Leon specimen is also. A radiometric age determination from a tuff overlying a partial skeleton of this taxon was given as 8.19 ± 0.16 Ma (Wagner, 1981). Aside from the meager Ixtapa local fauna from Chiapas (Ferrusquia, 1990), no other early Hemphillian vertebrates have previously been reported from all Mexico. Our earliest record of a possible South American immigrant is *Megalonyx* sp. However, McDonald (pers. comm.) argues that *Pliometanastes* evolved into *Megalonyx* after the former genus dispersed into North America. In this view *Megalonyx* would be a North American endemic taxon. It has been identified from four different localities in central Mexican states. Two lower molariform teeth considered to belong to this genus come from the village of Zietla in Hidalgo. These were found with specimens of *Dinohippus interpolatus* and *Agriotherium* ?*schneideri*. The age corresponds best to early, late Hemphillian. Another two lower molariform teeth were discovered in the fossil rich El Ocote local fauna from the San Miguel Allende basin in the state of Guanajuato. These probable *Megalonyx* teeth were recovered very low in the section with an associated late Hemphillian age fauna. Based on a fission track date from an ash overlying these teeth by about 3m, they are older than 4.8 Ma. At about the border of the states of Hidalgo and Mexico in the "La Plegaria" local fauna, a lower caniniform tooth and phalanx of *Megalonyx* was found. Faunal associates here representing an Hemphillian age include *Osteoborus cyonoides*, *Canis* cf.

ferox, *Agriotherium* cf. *schneideri*, *Teleoceras* cf. *fossiger*, *Dinohippus mexicanus*, *Neohipparion eurystyle*, *Nannippus minor* (= *Nannippus aztecus*) and *Prosthennops* sp. The fourth locality is the "La Hacienda" local fauna from near Tecolotlán located in the state of Jalisco. Here a lower molariform tooth and a carpal bone were recovered. It, too, comes from late Hemphillian deposits based on a radiometric age dating of 4.8 Ma. (^{40}Ar/ ^{39}Ar laser-fusion) and associated taxa. These taxa include *Notolagus velox*, *Osteoborus* cf. *cyonoides*, *Canis ferox*, *Teleoceras fossiger*, *Neohipparion eurystyle* and *Dinohippus mexicanus*. These finds of *Megalonyx* constitute some of the earliest as well as the southernmost ones in North America. Although no reported specimens of this genus come from outside the continent, it cannot be ruled out that *Megalonyx* was not an immigrant. Relative to this, it should be kept in mind that very few late Hemphillian age deposits have been reported from Middle America south of central Mexico through northern South America. As the Hemphillian-Blancan boundary in central Mexico has been placed at about 4.8 Ma (Kowallis *et al.*, 1998), if *Megalonyx* did disperse from South America, which is problematical, it had to be a little earlier than this date.

Marshall (1985), Webb (1985), and others have stated that *Glossotherium*, a large mylodontid ground sloth, entered North America from South America in the late Blancan. Marshall (1985) indicated its presence in Arizona, New Mexico and Florida at this time. Our records show its occurrence in central Mexico significantly earlier. Based on radiometric dating, it has been recognized in Guanajuato at 4.7 Ma, in the earliest Blancan. A partial fibula was found at the El Ocote locality. And at the nearby El Tanque locality a piece of a mandible showing the m2 alveolus, vertebrae and ribs, front and rear foot elements as well as dermal ossicles were recovered (Montellano & Carranza, 1986). It is generally agreed (e.g., Marshall, 1985) that *Glossotherium* walked across the Panamanian land bridge. If so, a connection would necessarily have existed 4.7 Ma. This is much earlier than he and others (see above) reported for the formation of the Panamanian Isthmus. It is now necessary to reevaluate all current evidences that relate to this important event. *Glossotherium* fossils dated at 4.7 Ma in Mexico become a very significant factor. Interestingly, Hoernle *et al.* (2002) postulated the Central American land bridge forming 4.6 Ma. Why more immigrants have not been found in Middle America at this time remains somewhat enigmatic. Lack of sufficient proper age deposits (or investigations thereof), the possible submerged condition of the land bridge at times, as well as topographic and vegetational barriers might all have played a role in this. Conceivably *Glossotherium*, *Pliometanastes*, *Thinobadistes* (and possibly *Megalonyx*) could have been strong swimmers. The ground sloths from the Antilles' islands indicate this. Hirschfeld (1985) implied that sloths had low metabolisms, and as Webb (1985) stated above, ground sloths must have had a wide tolerance for ecological conditions. Therefore, it is possible that these ground sloths crossed prior to the Central American land bridge

becoming a continuous structure; before more favorable conditions allowed for completely overland dispersals.

Following the arrival of *Glossotherium* in central Mexico, two other South American immigrants made their appearance. One was *Glyptotherium* and the other *Plaina*. ^{40}Ar/^{39}Ar dates based on single-crystal sanidine (Kowallis *et al.*, 1998) for both genera were given as 3.9 Ma. According to the time scale given by Lindsay (2001), this equates to the early Blancan. Earlier reports (e.g., Marshall, 1985; Webb, 1985) has the first named genus arriving in North America toward the end of the Blancan. Gallusha *et al.* (1984) stated that *Glyptotherium* as well as *Glossotherium* and N*eochoerus*, all South American immigrants, made their earliest known appearance in North America at the 111 Ranch locality in Arizona. A date for this occurrence was given at slightly less than 2.5 Ma. The central Mexican record of *Glyptotherium* is therefore more than one million years earlier. This is also true for the appearance of *Neochoerus* in central Mexico at 3.6 Ma. *Glyptotherium* is known from the San Miguel Allende basin in Guanajuato, where it was dated, and also from near Tecolotlán in Jalisco. It has been identified on the basis of portions of the carapace in Guanajuato and by isolated scutes in Jalisco where faunal associates include *Equus* cf. *E.* simplicidens, *Neochoerus* cf. *N. cordobai*, *Platygonus* sp. and *Camelops* sp. The scutes from probable late Blancan deposits in Jalisco show noticeable differences from the ones collected in Guanajuato. According to Gillette & Ray (1981), known North American glyptodonts all belong to the genus *Glyptotherium*. They recognize no more than five valid species.

Plaina, a pampathere, has been identified on the basis of isolated scutes at two localities in the San Miguel Allende basin in Guanajuato. It occurs with *Glyptotherium* at one of these sites, Arroyo Belén, where dates were run on associated volcanic ashes. The 3.9 Ma age resulted from this. Because of the similarity between isolated scutes, this material was earlier misidentified as *Pampatherium* (Miller & Carranza, 1999, 2001). But comparisons with illustrations of scutes of *Plaina* from Bolivia (Anaya & MacFadden, 1995), demonstrate that the Mexican specimens are most likely assignable to that genus. This marks the first report of *Plaina* from the late Tertiary of North America. In 1985 Edmund tentatively referred some scutes of Pleistocene age from the Mexican state of Puebla to the genus *Plaina*. A few isolated scutes from Cita Canyon in Texas housed in the Panhandle-Plains Historical Museum in Canyon, Texas, appear to belong to this genus as well. Despite all the fieldwork and study regarding the GABI, there is still the possibility of new South American taxa being discovered in Middle America including central Mexico.

Of the late Tertiary mammals found in central Mexico, the capybara, *Neochoerus*, has the best representation. Much cranial as well as postcranial material has been identified (Carranza & Miller, 1988). While most of this is from older Blancan deposits of the San Miguel Allende basin in Guanajuato, with a fission track date of 3.6 Ma, other material comes from Jalisco and appears to be of late Blancan age. There it is associated with the younger glyptothere species noted above. Two species were identified in Guanajuato, a larger and a smaller form (Carranza & Miller, 1988). Both probably represent new species of *Neochoerus*, but only the larger was given a new species name, *N. cordobai*. A late Blancan species of *Neochoerus*, *N. dichroplax*, was named by Ahearn & Lance (1980). It was reported from Arizona, including the 111 Ranch locality, as well as from Florida. The smaller Mexican species, based upon the small amount of material presently available, does not appear to be assignable to that species (Carranza & Miller, 1988).

It is noteworthy that no South American immigrant taxa of late Tertiary age, with the exception of the recent identification of *Pliometanastes* from northeastern Mexico, have been reported from Mexico north of the Transmexican Volcanic Belt. The late Hemphillian Yepómera deposits of Chihuahua and their contained vertebrates are both diverse and numerous. Additionally, some Blancan vertebrate sites are also known from the general area (Lindsay, 1984). Yet, none have yielded South American animals to date. The only reported South American form comes from a later time (early Pleistocene). It is *Myrmecophaga,* a giant anteater, from the northwest corner of the country in Sonora (Shaw & McDonald, 1987).

The question could be asked why late Tertiary South American immigrants in Mexico are relatively scarce? Almost all finds represent isolated bones and teeth, or fragments of carapaces in the case of armored edentates. This might be seen as strange when so much material is known of South American immigrants in the United States. But, the great bulk of this material is Pleistocene in age. Considering the much more extensive searching of both late Tertiary and Pleistocene deposits that has taken place north of Mexico, the results should not be surprising. Actually, relatively little material of late Tertiary age is known for South American immigrants in the northern part of the continent when compared to that for indigenous animals. These immigrants could reasonably be expected to be more numerous in the southern part of the continent though. However, mitigating factors exist. South of central Mexico to the northern limit of South America, there are not extensive exposures of sediments. And despite the increased searching in central Mexico, the amount of vertebrate paleontological field work relating to the late Tertiary must still be considered in initial stages. With continued research, though, additional South American immigrants will undoubtedly be found. This will certainly aid in a clearer understanding of details relating to the Great American Biotic Interchange. But the presence of *Glossotherium*, *Glyptotherium*, *Plaina*, and *Neochoerus* in central Mexico from 4.7 to 3.6 Ma strongly suggests a Panamanian land bridge, if only an intermittent one.

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