

THE GREAT AMERICAN BIOTIC INTERCHANGE IN FLORIDA

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Late Neogene vertebrate faunas from Florida provide the most complete record of South American mammals and birds that arrived in temperate North America during the Great American Biotic Interchange (GABI). The first major pulse of the GABI began in the early Hemphillian (late Miocene, ~9 Ma), defined in part on the first appearance of two sloths of South American origin, the megalonychid *Pliometanastes* and the mylodontid *Thinobadistes*. The type localities of *Pliometanastes protistus* (McGehee Farm) and *Thinobadistes segnis* (Mixson's Bone Bed) are both earliest Hemphillian (8-9 Ma) sites from northern Florida. *Pliometanastes* evidently gave rise to *Megalonyx* in the late Hemphillian. The latest Hemphillian (~5 Ma) Palmetto Fauna documents the earliest occurrence of *Megalonyx* in Florida. The second major pulse of the GABI occurred during the late Pliocene and early Pleistocene, from 2.7 to 1.5 Ma. The late Blancan is defined by the first appearance in temperate North America of a diverse assemblage of vertebrates from South America, including ten genera, all of which occur in Florida during the late Blancan: the giant flightless bird *Titanis*, the glyptodont *Glyptotherium*, the armadillos *Dasybus* and *Pachyarmatherium*, the pampathere *Holmesina*, the mylodontid *Glossotherium*, the megatheriid *Eremotherium*, the porcupine *Erethizon*, and the capybaras *Hydrochaeris* and *Neochoerus*. During the late Blancan, *Titanis*, *Dasybus*, *Pachyarmatherium*, *Holmesina*, *Eremotherium*, and *Hydrochaeris* are primarily restricted to Florida, whereas *Glyptotherium*, *Glossotherium*, *Erethizon*, and *Neochoerus* are more widespread, occurring in Florida as well as the western United States. These ten genera have their earliest occurrence in early late Blancan (2.2-2.7 Ma) sites from Florida and/or the southwestern United States. Four genera of South American mammals arrived in temperate North America somewhat later: *Paramylodon* and *Desmodus* in the latest Blancan (1.8-2.2 Ma), *Nothrotheriops* in the early Irvingtonian (1.6-1.8 Ma), and *Didelphis* in the medial Irvingtonian (~0.8 Ma).

Key Words: Florida; Great American Biotic Interchange; Miocene; Pliocene; Pleistocene; Hemphillian; Blancan; Irvingtonian

INTRODUCTION

The biotas of North America and South America were vastly altered in the Late Cenozoic by the connection of these two continents at the Panamanian Isthmus and the subsequent intermixing of their faunas and floras, an event variously named the Great American Interchange, Great American Faunal Interchange, Great American Biotic Interchange, or just the Interchange. Most workers now use the term Great American Biotic Interchange (hereafter shortened to GABI), coined by Stehli and Webb (1985). Although the mixing of faunas from North and South America has been known for more than a century, George Gaylord Simpson (1950) was one of the first authors to discuss the GABI in the context of a profound biogeographic event that dramatically changed the biotas of these two continents. David Webb was another early pioneer who investigated the GABI in

terms of its theoretical context. Webb's (1976) landmark paper on the mammalian faunal dynamics of the Interchange stimulated considerable additional research on the GABI.

Beginning in the late Miocene and continuing through the end of the Pleistocene, Florida has the richest record in North America of vertebrate taxa involved in the Great American Biotic Interchange. Florida has played a key role in understanding the history of the Interchange vertebrate fauna in temperate North America (Webb 1974, 1976; Morgan & Hulbert 1995). Paleontologists in the late nineteenth and first half of the twentieth centuries documented the presence of South American mammals in Florida late Pleistocene faunas. Leidy (1889) named *Glyptodon septentrionalis*, an animal now recognized as the pampathere *Holmesina septentrionalis* (Simpson 1930a), from the Peace River in southern Florida. Simpson (1928) named the capybara *Hydrochaeris holmesi* from the late Pleistocene Sabretooth Cave in central Florida and the large arma-

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dillo *Tatu* (= *Dasybus*) *bellus* and the glyptodont *Boreostracon* (= *Glyptotherium*) *floridanus* from the Seminole Field Fauna near St. Petersburg along the central Gulf Coast (Simpson 1929a). Most of these early discoveries were from late Pleistocene (Rancholabrean) sites, and thus post-Interchange; however, they provided ample evidence that Florida supported a rich Interchange fauna.

Beginning in the early 1960s and continuing through the present, large samples of Interchange vertebrates have been collected from sites throughout Florida, representing both the early heralds of the Interchange in the late Miocene and the time of maximum faunal interchange in the late Pliocene and early Pleistocene. It is no coincidence that this 40-year period of discovery of the Interchange fauna in Florida corresponds with David Webb's residence at the Florida State Museum/Florida Museum of Natural History. Early in his career at the University of Florida, Webb became keenly interested in the Interchange and the strange and wonderful beasts that populated Florida as a result of the GABI, including ground sloths, glyptodonts, giant armadillos, capybaras, and huge predatory birds. One of the first and most important Interchange discoveries was the giant flightless phorusrhacid bird *Titanis walleri* at the late Blancan Santa Fe River 1 site (Brodkorb 1963). The association of *Titanis* and several other genera of South American immigrants with the last of the three-toed horses, *Nannippus peninsulatus*, alerted Webb to the Blancan age of the Santa Fe River sites, although Brodkorb (1963) originally regarded *Titanis* as Pleistocene. Shortly thereafter, the discovery of a second late Blancan Interchange site in northern Florida, Haile 15A, added more information to the early history of the GABI in Florida (Robertson 1976), including partial skeletons of the small pampathere *Kraglievichia* (= *Holmesina*) *floridanus* and the small mylodontid sloth *Glossotherium chapadmalense*. Work at the late Miocene (early Hemphillian) McGehee Farm site in the early to mid 1960s led to the discovery and description of the oldest megalonychid sloth in North America, *Pliometanastes protistus* (Hirschfeld & Webb 1968). Through the field studies of Webb and many of his graduate students, other important discoveries of Florida Hemphillian, Blancan, and Irvingtonian Interchange faunas came in rapid succession during the late 1960s (Coleman 2A, Inglis 1A, Kissimmee River, Pool Branch,), 1970s (Crystal River Power Plant, Haile 16A, Payne Creek Mine), 1980s (Haile 19A, Haile 21A, Leisey Shell Pit, Macasphalt Shell Pit, Moss Acres, Haile

7C, De Soto Shell Pit), 1990s (Whidden Creek, Inglis 1C), and into the 2000s (Tyner Farm, Haile 7G).

Along with these new discoveries of Interchange faunas, notably in Florida by Dave Webb and his students, major advances in geochronologic techniques, especially radioisotopic dating and paleomagnetic stratigraphy, led to a flurry of studies on the GABI in the 1970s and 1980s (e.g., Patterson & Pascual 1972; Webb 1976, 1978, 1985; Marshall et al. 1979, 1982; Simpson 1980; Galusha et al., 1984; Marshall 1985), culminating in the 1985 book "The Great American Biotic Interchange," edited by Frank Stehli and David Webb. The dispersal of South American mammals into North America has been accorded great significance in mammalian biochronology (e.g., Woodburne & Swisher 1995; Bell et al. 2004; Tedford et al. 2004). The beginning of the Hemphillian North American Land Mammal Age (NALMA) in the late Miocene (about 9 Ma) is defined in part on the first appearance of two ground sloths of South American origin, *Pliometanastes* and *Thinobadistes*. The late Blancan NALMA (late Pliocene, about 2.7 Ma) is defined on the first appearance in temperate North America of mammals involved in the second phase of the GABI (e.g., *Glyptotherium*, *Glossotherium*, *Nechoerus*, and *Erethizon*).

With the exception of several papers by Webb (1991, 1997), there has been little work on the GABI in temperate North America during the past 15 years, although there have been several important papers on Blancan Interchange faunas from central Mexico (Carranza-Castañeda & Miller 2004; Flynn et al 2005). Most of the papers on the GABI from the 1970s and 1980s stressed either geochronology or theoretical ecological and biogeographic aspects of the Interchange. Few of these papers provided specific information on the species of vertebrates involved in the Interchange or on the sites from which they were collected. My intention here is to provide information on the geology and biochronology of the key Florida Interchange sites and to review the taxonomy, distribution, and biochronology of the Interchange vertebrate fauna of Florida.

MATERIALS AND METHODS

All genera and species of South American immigrant mammals and birds involved in the Great American Biotic Interchange known from Late Neogene sites in Florida are reviewed, covering not only species that immigrated to Florida from the late Miocene (early

Ma	Epoch	NALMA	FLORIDA	NORTH AMERICA (exclusive of Florida)	
1.0	PLEISTOCENE early med	IRVINGTONIAN early m	McLeod		
			Haile 21A	Coleman 2A	Gilliland TX Holloman OK *
			Haile 16A	Leisey S.P.	Mesilla NM ABD CA El Golfo MX
2.0	PLIOCENE late	BLANCAN late	Inglis 1A	Curtis Ranch AZ Mesilla B NM	
			Haile 15A	De Soto S. P.	Blanco Cal Tech AZ ABD CA
			SF R.1	Macasphalt	111 Ranch AZ Wolf Ranch AZ
3.0	PLIOCENE early	BLANCAN early	Haile 7C	Mesilla A NM Pearson Mesa NM	
			Kiss.R.	Cita Canyon TX Hudspeth TX	
				Red Light TX #	
4.0	PLIOCENE early	BLANCAN early			
5.0	MIOCENE late	HEMPHILLIAN e. late	Palmetto	Black Rascal Cr. CA	
					Coffee Ranch TX x
					ZX Bar NE Optima OK
6.0	MIOCENE late	HEMPHILLIAN e. late			
					Box T TX Chamita NM +
					Oshkosh NE Aphelops Draw NE
7.0	MIOCENE late	HEMPHILLIAN e. late	Moss Acres		
			With. R. 4A,X		
8.0	MIOCENE late	HEMPHILLIAN e. late	Mixson's		
					Siphon Canal CA
9.0	MIOCENE late	HEMPHILLIAN e. late	McGehee Farm		
			Haile 19A		

Figure 1. Chronology of important Hemphillian, Blancan, and Irvingtonian Interchange faunas from Florida and correlative faunas from the western U.S. Faunas included within rectangle marked “+” are late early Hemphillian (Hh2). Faunas included within rectangle marked “x” are early late Hemphillian (Hh3). Faunas included within rectangle marked “#” are early late Blancan (about 2.7 Ma). Faunas included within rectangle marked “*” are early Irvingtonian (1.0-1.6 Ma). Abbreviations used in table: ABD (Anza-Borrego Desert), Kiss. (Kissimmee), R. (River), SF (Santa Fe), S. P. (Shell Pit), With. (Withlacoochee).

Hemphillian) through the late Pleistocene (Rancholabrean), but also species that evolved in situ in North America from species of South American origin. The primary focus is on the mammals from the two main phases of the Interchange, late Miocene and late Pliocene/early Pleistocene.

Florida is widely recognized to have an extremely diverse and abundant Late Neogene vertebrate fossil record (Hulbert 2001); however, the biostratigraphic importance of Florida faunas is often downplayed because of the overall lack of long stratigraphic sections that can be physically correlated and the absence of associated geochronologic data such as radioisotopic

dates and paleomagnetic stratigraphy. The age of most Florida Late Neogene vertebrate faunas has been determined by biochronologic correlations with similar faunas from western North America that have associated geochronologic data (Fig. 1). Many Florida Hemphillian, Blancan, and Irvingtonian vertebrate faunas are quarry samples collected from restricted stratigraphic units, generally several meters or less in thickness, and over a very limited area, seldom more than several thousand square meters. Most Florida faunas are local faunas in the classic sense (narrow stratigraphic range and limited areal extent), are synchronous (not time averaged), and sample a limited range of paleoenvironments. More-

over, many Florida sites have remarkably abundant and diverse faunas containing well preserved fossils (e.g., Mixson's Bone Bed, Moss Acres, Haile 7C, Inglis 1A, Leisey Shell Pit, Haile 21A).

Abbreviations used in the text and tables are: FLMNH (Florida Museum of Natural History); FSM (Florida State Museum, name of the FLMNH before 1985); FAD (first appearance datum); GABI (Great American Biotic Interchange); LF (Local Fauna); Ma (Mega-annum or millions of years before present); NALMA (North American land mammal age).

CHRONOLOGY

The Miocene/Pliocene and Pliocene/Pleistocene boundaries, the subdivisions of the epochs, and the boundaries of the geomagnetic chrons and subchrons follow Berggren et al. (1995). The Miocene/Pliocene boundary is at 5.32 Ma and the Pliocene/Pleistocene boundary is located near the top of the Olduvai Subchron at 1.81 Ma. The late Miocene (5.3-11.2 Ma) is the only subdivision of the Miocene known to contain Interchange vertebrates, which first appeared about 9 Ma. The boundary between the early and late Pliocene is placed at the boundary between the Gilbert and Gauss Chrons at 3.58 Ma (early Pliocene, 3.6-5.3 Ma; late Pliocene, 1.8-3.6 Ma). The Pleistocene is subdivided into the early, medial, and late Pleistocene. The boundary between the Matuyama and Brunhes Chrons at 0.78 Ma separates the early Pleistocene (0.8-1.8 Ma) and medial Pleistocene (0.13 Ma-0.8 Ma). The beginning of the late Pleistocene at 0.13 Ma is defined by the onset of the last (Sangamonian) interglacial. I follow Woodburne and Swisher (1995) for use of the age terms early, medial, and late for subdivisions of the epochs (e.g., medial Pleistocene) and NALMAs (e.g., late Blancan).

Definitions and boundaries of the three North American land mammal ages (NALMA) that comprise the time period of the GABI (Hemphillian, Blancan and Irvingtonian) follow Tedford et al. (2004) for the Hemphillian and Bell et al. (2004) for the Blancan and Irvingtonian, with several modifications discussed below. Geochronologic and biochronologic data are consistent with an age of 9 Ma for the beginning of the Hemphillian NALMA in North America (Woodburne & Swisher 1995; Tedford et al. 2004), defined in part on the first appearance of two genera of ground sloths of South American origin, *Pliometanastes* and *Thinobadistes*. These two sloths are best represented and have their type localities in very early Hemphillian

(8-9 Ma; Hh1 of Tedford et al. 2004) sites in Florida, although both genera occur in early Hemphillian sites in the western United States (Hirschfeld & Webb 1968; Hirschfeld 1981; Webb 1989). The late early Hemphillian (~7.0-7.5 Ma; Hh2 of Tedford et al. 2004) is characterized in part by the appearance at about 7.5 Ma of the Eurasian immigrant carnivores *Enhydritherium*, *Indarctos*, and *Machairodus*. Florida late early Hemphillian Interchange faunas are Moss Acres, Withlacoochee River 4A, and Withlacoochee River 4X. All three of these carnivore genera are present in the Withlacoochee River 4A LF and *Enhydritherium* occurs at Moss Acres (Lambert 1997). Although the immigrant carnivores that characterize the late early Hemphillian are absent from Withlacoochee River 4X, its proximity and similarity to the Withlacoochee River 4A LF indicate that these two faunas are essentially the same age. Late Hemphillian faunas (~4.9-7.0 Ma; Hh3 and Hh4 of Tedford et al. 2004) are characterized by the first appearance of several Old World immigrants, including the carnivores *Agriotherium* and *Plesiogulo*, and the cervid *Eocoileus*. These taxa are present in the latest Hemphillian Palmetto Fauna (also known as the Upper Bone Valley Fauna) from the Bone Valley Formation in central Florida (Webb & Hulbert 1986; Morgan 1993, 1994; Webb 2000; Webb et al. in press). The Palmetto Fauna records the earliest Florida occurrence of *Megalonyx*. The end of the Hemphillian is characterized by a major extinction event, including the disappearance of the families Rhinocerotidae and Protoceratidae, the horses *Hipparion*, *Neohipparion*, *Pseudhipparion*, and *Astrohippus*, and the carnivores *Agriotherium*, *Machairodus*, and *Plesiogulo*.

Lindsay et al. (2002) placed the Hemphillian/Blancan boundary at about 4.9 Ma based on the earliest occurrence of the microtine rodent *Mimomys* in the Panaca LF in Nevada. Bell et al. (2004) defined the beginning of the Blancan (~4.9 Ma) on the first appearance of the microtine rodents *Ophiomys*, *Ogmodontomys* (both considered subgenera of *Mimomys* by Repenning, 1987), and *Mimomys*. I follow Woodburne and Swisher (1995), Lindsay et al. (2002), and Bell et al. (2004) in placing the Hemphillian/Blancan boundary in the early Pliocene at about 4.9 Ma. The beginning of the Blancan NALMA in temperate North America does not have an Interchange component since there are no new appearances of South American mammals until the late Blancan. *Megalonyx* is the only genus of South American ancestry that occurs in temper-

ate North American early Blancan faunas. The early Blancan (2.7-4.9 Ma) is the only interval during the last 9 million years that is not represented by Interchange mammals in Florida. The early Pliocene was a period of high sea level, and consequently vertebrate faunas of this age from Florida are exclusively marine (Morgan 1993, 1994; Allmon et al. 1996). The onset of the main pulse of the GABI in temperate North America is characterized by the first appearance of South American immigrants in the southwestern United States in the upper Gauss Chron, between about 2.6 and 2.8 Ma (Galusha et al. 1984; Marshall 1985). The date of 2.7 Ma is generally stated as the first appearance datum (FAD) for Neotropical immigrants in North America, as well as the boundary between the early and late Blancan (Woodburne & Swisher 1995). Two South American xenarthrans (*Glyptotherium* and *Glossotherium*) and two South American caviomorph rodents (*Nechoerus* and *Erethizon*) first appear in temperate North America in several sites in the southwestern United States at about 2.7 Ma. *Glossotherium* and *Nechoerus*, as well as *Dasyus* and *Holmesina*, occur in the early Matuyama Chron (2.2-2.6 Ma) in the Macasphalt Shell Pit LF in southern Florida (Hulbert 1987; Morgan & Ridgway 1987; Jones et al. 1991; Morgan & Hulbert 1995). Other Florida late Blancan sites document the presence of three additional genera of South American immigrants, the giant flightless bird *Titanis*, the giant ground sloth *Eremotherium*, and the strange armadillo *Pachyarmatherium*. These sites lack external age control except for biochronology, but the association of South American immigrants with *Nannippus* indicates an age of 2.2-2.7 Ma based on comparisons with southwestern faunas.

Typical Irvingtonian (and younger) genera such as *Mammuthus* and *Microtus* did not appear in North America until after 1.8 Ma. Several recent studies (Morgan & Lucas 2003; Bell et al. 2004) have advocated defining the beginning of the Irvingtonian on the first appearance of *Mammuthus*, a Eurasian immigrant, although these authors differ somewhat on the timing of the FAD for *Mammuthus*. The earliest well-dated faunas in North America containing *Mammuthus*, Tijeras Arroyo and Mesilla Basin Fauna C in New Mexico (Vanderhill 1986; Lucas et al. 1993 1999; Morgan & Lucas 2003), have associated radioisotopic dates of about 1.6 Ma, which is older than the date of 1.35 Ma recognized by Bell et al. (2004). The early Irvingtonian Leisey Shell Pit in Florida has one of the earliest North

American samples of *Mammuthus* (Webb & Dudley 1995). Other genera that have their first appearance in the early Irvingtonian (Morgan & Hulbert 1995) are the ground sloth *Nothrotheriops*, a South American immigrant, and the giant beaver *Castoroides* and the camelid *Palaeolama*, which are both native North America genera.

FLORIDA INTERCHANGE FAUNAS

HEMPHILLIAN

McGehee Farm.—McGehee Farm is located about 5 km north of Newberry, Alachua County, northern peninsular Florida (Fig. 2, site 1). The McGehee Farm LF, derived from the Alachua Formation, contains more than 50 species of vertebrates representing estuarine, freshwater, and terrestrial environments (faunal list in Hirschfeld & Webb 1968). The mammalian fauna consists of at least 25 species, including many age-diagnostic taxa suggesting an early Hemphillian age. McGehee Farm is the type locality for the oldest North American megalonychid ground sloth, *Pliometanastes protistus* (Hirschfeld & Webb 1968). Webb (1989) also identified the mylodontid ground sloth *Thinobadistes segnis* from McGehee Farm, making this one of only three sites in North America that document the association of *Pliometanastes* and *Thinobadistes*. McGehee is the oldest record of *Thinobadistes*. McGehee Farm and the latest Clarendonian (9.0-9.5 Ma) Love Bone Bed have very similar mammalian faunas (Webb et al. 1981). McGehee Farm and Love share the borophagine canids *Epicyon haydeni* and *E. saevus* (Baskin 1998; Wang et al. 1999), the equids *Protohippus gidleyi*, *Calippus elachistus*, *Neohipparion trampasense*, *Pseudhipparion skinneri*, *Nannippus westoni*, *Cormohipparion ingenuum*, and *Cormohipparion plicatile* (Webb & Hulbert 1986; Hulbert 1988a, 1988b, 1993), the tapir *Tapirus webbi* (Hulbert this volume), and the rhinocerotids *Teleoceras proterum* and *Aphelops malacorhinus* (Webb et al. 1981; Prothero 1998). The most significant difference between these two faunas is the presence of ground sloths at McGehee and their absence at the Love Site. The diverse vertebrate fauna from the Love Site is so abundantly sampled that the absence of sloths is almost certainly significant, and indicative of a pre-Hemphillian age (i.e., latest Clarendonian). The similarity of McGehee Farm to the Love Site suggests that the former site is very early Hemphillian in age (Hh1, 8.5-9 Ma).

Haile 19A.—The Haile 19A site was found in the

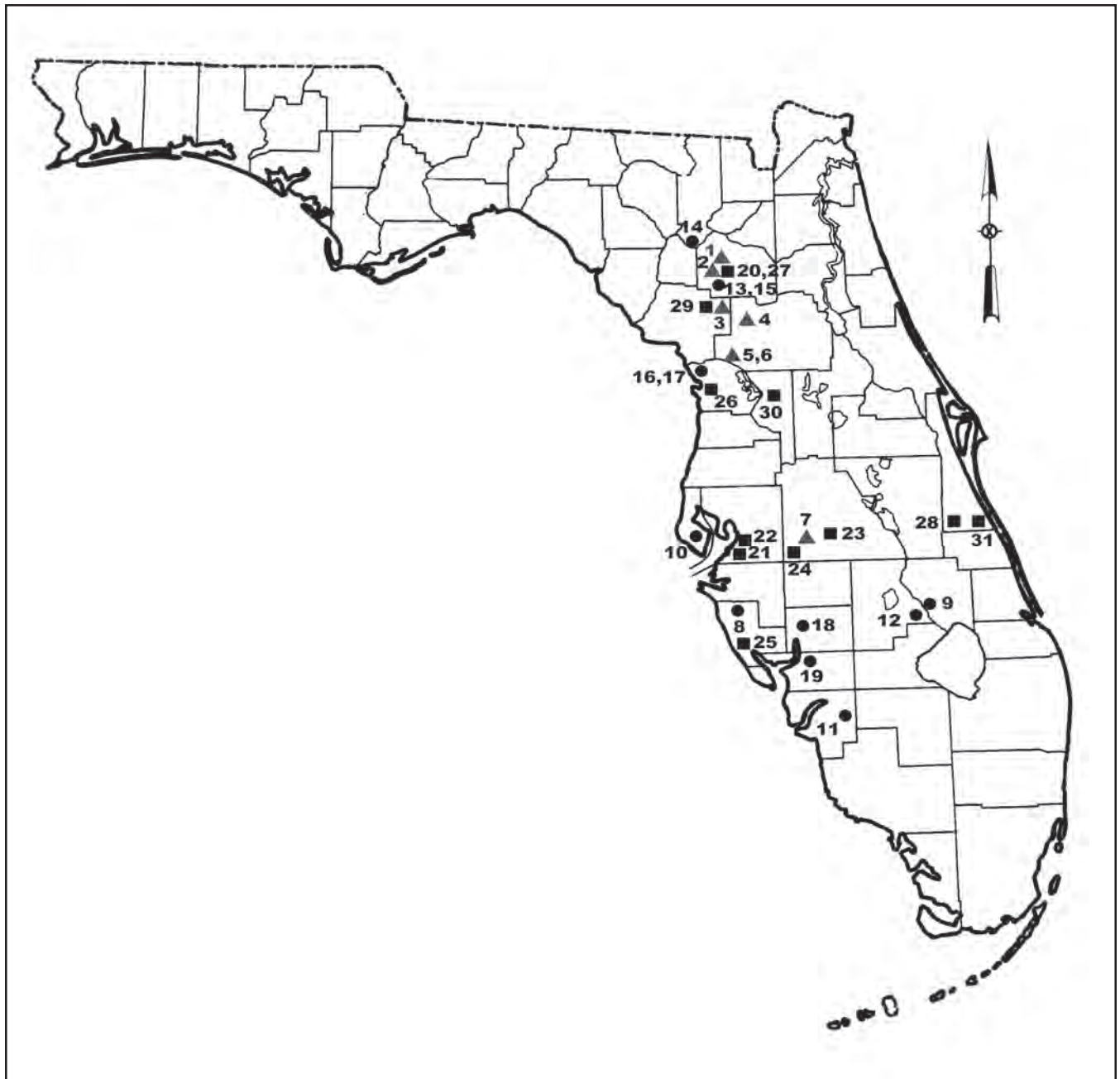


Figure 2. Important Hemphillian (triangles), Blancan (circles), and Irvingtonian (squares) Interchange faunas from Florida. Hemphillian: 1. McGehee Farm, Alachua County; 2. Haile 19A, Alachua County; 3. Mixson's Bone Bed, Levy County; 4. Moss Acres, Marion County; 5. Withlacoochee River 4A, Marion County; 6. Withlacoochee River 4X, Marion County; 7. Palmetto, Polk County. Blancan: 8. Macasphalt Shell Pit, Sarasota County; 9. Kissimmee River, Okeechobee County; 10. St. Petersburg Times, Pinellas County; 11. Lehigh Acres, Lee County; 12. Brighton Canal, Highlands County; 13. Haile 15A, Alachua County; 14. Santa Fe River 1, Columbia/Gilchrist Counties; 15. Haile 7C, Alachua County; 16. Inglis 1A, Citrus County; 17. Inglis 1C, Citrus County; 18. De Soto Shell Pit, De Soto County; 19. Forsberg Shell Pit, Charlotte County. Irvingtonian: 20. Haile 16A, Alachua County; 21. Leisey Shell Pit, Hillsborough County; 22. Apollo Beach, Hillsborough County; 23. Pool Branch, Polk County; 24. Payne Creek Mine, Polk County; 25. Rigby Shell Pit, Sarasota County; 26. Crystal River Power Plant, Citrus County; 27. Haile 21A, Alachua County; 28. Tucker Pit, Brevard County; 29. McLeod, Levy County; 30. Coleman 2A, Sumter County; 31. Sebastian Canal, Brevard County.

Haile quarries, a large complex of commercial limerock quarries located about 5 km northeast of Newberry and about 1 km east of the McGehee Farm site, Alachua County, Florida (Fig. 2, site 2). The individual Haile quarries are numbered, and sites within a single quarry are distinguished by a letter designation (e.g., Haile 19A is the first site found in quarry 19; there are four additional sites in this same quarry named Haile 19B-E that range in age from Hemphillian to Rancholabrean). The Haile 19A site, now completely destroyed by mining operations, consisted of sands and clays of the Alachua Formation that filled a sinkhole in marine Eocene limestone of the Crystal River Formation. The fauna is dominated by nearshore marine vertebrates, the most abundant of which is the long-snouted estuarine crocodile *Gavialosuchus americanus* (Morgan 1986). *Pliometanastes protistus* is represented by two teeth and three phalanges. Haile 19A shares several age-diagnostic species carnivores and horses with Love Bone Bed and McGehee Farm. The presence of *Pliometanastes* and *Calippus* cf. *C. hondurensis* at Haile 19A and McGehee Farm (Hulbert 1988a) distinguishes these faunas from the Love Bone Bed LF, and indicates a very early Hemphillian age.

Mixson's Bone Bed.—Mixson's Bone Bed near Williston in Levy County in northern Florida (Fig. 2, site 3), discovered in 1884, was the first Miocene vertebrate locality described from Florida (Leidy 1885, 1886, 1888; Leidy & Lucas 1896). The site was worked between 1884 and 1890 by various collectors for the U. S. Geological Survey and again in 1914 by E. H. Sellards for the Florida Geological Survey. The largest collection from Mixson's Bone Bed was amassed in the late 1930s and early 1940s by Frick field parties under the direction of Ted Galusha. There is some discrepancy concerning the exact spelling of this locality. The first time the name of this site appears in the literature, Leidy (1888:309) called it "Mixson's bone-bed." However, in a monograph on the vertebrate fossils from this same site, Leidy and Lucas (1896:9) stated that the fossils were collected "...on the plantation of J. M. Mixon..." Several other places in the same paper, Leidy and Lucas (1896) referred to this locality as "Mixon" without the "s" and that spelling has been used in several subsequent papers. Simpson (1929b, 1930b) emphatically stated that the correct spelling is Mixson's Bone Bed, noting that "This name should be Mixson. It has been misspelled in all previous publications."

Mixson's Bone Bed is the type locality of the Alachua Formation, the same geologic unit from which

the Love Bone Bed, McGehee Farm, and Haile 19A vertebrate faunas were derived. The only available faunal lists are those of Leidy and Lucas (1896) and Simpson (1929b, 1930b), published before the large collections were made by Frick field parties. Mixson's is the type locality for the earliest North American mylodontid sloth *Thinobadistes segnis* (Hay 1919; Webb 1989). Hay (1919) thought *Thinobadistes* was Pleistocene in age, but the large sample of this genus recovered from Mixson's by Frick field crews confirms its late Miocene age (Webb 1989). Mixson's Bone Bed has many age-diagnostic early Hemphillian mammals: the borophagine canids *Epiyon haydeni* and *Borophagus pugnator* (Wang et al. 1999); the equids *Protohippus gidleyi*, *Calippus hondurensis*, *Nannippus westoni*, *Cormohipparion ingenuum* (type locality), and *C. plicatile* (type locality) (Hulbert 1988a, 1988b, 1993); the rhinocerotids *Teleoceras proterum* (type locality) and *Aphelops malacorhinus* (Prothero 1998), the large camelid *Aepycamelus major* (type locality), and the gomphotheriid proboscidean *Amebelodon floridanus* (type locality). Mixson's shares most of these mammals with the latest Clarendonian Love Bone Bed and the earliest Hemphillian McGehee Farm. Early Hemphillian taxa present at Mixson's and McGehee, but absent from the Love Site include *Thinobadistes segnis* and *Calippus hondurensis*. The presence of *Borophagus pugnator* (= *Osteoborus galushai* Webb 1969) and the somewhat more advanced characters in certain of the equid lineages (Hulbert pers. comm.), suggests that Mixson's Bone Bed is slightly younger than McGehee Farm, probably ~8.0-8.5 Ma (Hulbert 2001).

Moss Acres.—The Moss Acres Racetrack site is located on a horse farm northwest of Ocala and about 6 km east of Morriston in northwestern Marion County, Florida (Fig. 2, site 4). The fauna was derived from a massive clay deposit of the Alachua Formation and lacks a marine component. Unlike most other Florida early Hemphillian sites, many of the vertebrate fossils from Moss Acres show some articulation (Lambert 1994, 1997). Moss Acres produced a partial articulated skeleton of *Pliometanastes protistus*. Hulbert (1988a) and Lambert (1997) published faunal lists of the Moss Acres LF, which is most similar to the Withlacoochee River 4A LF, indicating a late early Hemphillian age (Hh2, 7.0-7.5 Ma). Mammalian taxa shared by Moss Acres and Withlacoochee River 4A, but not present in earliest Hemphillian faunas from Florida are: the giant otter *Enhydritherium terraenovae* (Berta & Morgan 1985; Lambert 1997), the canid *Borophagus orc* (Webb 1969;

Wang et al. 1999), the equids *Calippus maccartyi* (type locality) *Nannippus aztecus*, *Nannippus morgani*, and *Neohipparion eurystyle* (Hulbert 1988a, 1988b; 1993), and the large rhinoceros *Aphelops mutilus*. *Enhydritherium* is one of several Old World immigrant carnivore genera that first appears in North America in the late early Hemphillian (Tedford et al. 2004). The shovel-tusked gomphothere from Moss Acres, *Amebelodon britti* (type locality), represents the earliest record of the subgenus *Amebelodon* (*Konobelodon*), which became extinct in the late Hemphillian (Lambert 1990). Hulbert (1988b) observed slight differences in the grade of evolution between several species of horses from Moss Acres and Withlacoochee River 4A; however, he regarded the two sites as approximately contemporaneous late early Hemphillian faunas.

Withlacoochee River 4A and 4X.—Withlacoochee River 4A and 4X (Fig. 2, sites 5, 6) are both underwater sites located in the Withlacoochee River about 10 km southeast of Dunnellon in southwestern Marion County. The two Withlacoochee River sites were excavated by SCUBA teams from the FSM in the late 1960s and early 1970s, and were derived from clay-filled sinkholes formed in the marine Eocene Inglis Formation (Webb 1969). These two sites were deposited in separate sinkholes located several hundred meters apart and thus their faunal composition is slightly different, although they are almost certainly contemporaneous. Withlacoochee River 4A LF is the better known of the two faunas (Hirschfeld & Webb 1968; Webb 1969; Wolff 1977; Becker 1985; Berta & Morgan 1985; Hulbert 1988a, 1988b; 1993). Becker (1985) published a faunal list for this site, including more than 20 mammalian taxa, and Hulbert (1993) updated the identifications of the equids. Withlacoochee River 4A is one of the few sites that documents the co-occurrence of *Pliometanastes* and *Thinobadistes*. Hirschfeld and Webb (1968) referred a mandibular symphysis to *Pliometanastes protistus*, and substantial additional material of this species was collected after the publication of their paper (see account of *Pliometanastes* below). Withlacoochee River 4X is the type locality of the large species *Thinobadistes wetzeli*, and there are also several specimens of *T. wetzeli* from Withlacoochee River 4A (Webb 1989). Age-diagnostic early Hemphillian mammals from Withlacoochee River 4A are: *Enhydritherium terraenovae* (Berta and Morgan 1985); *Borophagus* (= *Osteoborus*) *orc* (type locality) and *B. pugnator* (Webb 1969; Wang et al. 1999); the large ursid *Indarctos* (Wolff 1977); the sabercat

Machairodus; the equids *Protohippus* cf. *P. gidleyi*, *Calippus maccartyi*, *Neohipparion eurystyle*, *Nannippus morgani* (type locality), and *Nannippus aztecus* (Hulbert 1988a; 1993); and the large rhinoceros *Aphelops mutilus*. The presence of the immigrant carnivore genera *Enhydritherium*, *Indarctos*, and *Machairodus* establishes a late early Hemphillian age (Hh2, 7.0-7.5 Ma; Tedford et al. 2004). Withlacoochee River 4X shares *Thinobadistes wetzeli*, *Borophagus pugnator*, *Aphelops mutilus*, and *Neohipparion eurystyle* with Withlacoochee River 4A, indicating a similar age.

Palmetto Fauna.—The Palmetto Fauna (also known as the Upper Bone Valley Fauna) is composed of a series of sites collected from commercial open-pit mines in the Bone Valley Phosphate Mining District in Polk and Hardee Counties in central Florida (Fig. 2, site 7). The Palmetto Fauna consists of a diverse assemblage of marine, estuarine, freshwater, and terrestrial vertebrates of latest Hemphillian age derived from phosphatic gravel deposits in the upper part of the Bone Valley Formation (Webb & Hulbert 1986; Morgan 1994; Webb et al. in press). Among Florida Hemphillian sites, the Palmetto Fauna is most like western faunas because it was collected over a fairly large area and through a stratigraphic thickness of 10 m or more, and thus the fauna is time averaged and samples a variety of habitats. The first collections from the Bone Valley area date back to the early 1900s (Simpson 1929b, 1930b), but it was not until the mid-1960s and thereafter that the complex stratigraphic relationships of the Bone Valley Formation began to be unraveled through the discovery of in-place vertebrate samples representing four major faunal assemblages, the late Barstovian Bradley Fauna, the early Clarendonian Agricola Fauna, the early Hemphillian Four Corners Fauna, and the latest Hemphillian Palmetto Fauna (Webb & Crissinger 1983; Webb & Hulbert 1986; Morgan 1994; Hulbert et al., 2003). Several diverse in-place samples of the Palmetto Fauna, including the Whidden Creek LF in the Gardiner Mine, allow detailed biochronologic comparisons with other late Hemphillian faunas in the western US (Morgan 1994; Webb et al. in press). The megalonychid ground sloth *Megalonyx curvidens* is well represented in the Whidden Creek LF (Webb et al. in press). Four Eurasian immigrant carnivores are indicative of late Hemphillian faunas (Hh3/Hh4; Tedford et al. 2004): the large ursid *Agriotherium*, the sabercat *Megantereon* (Berta & Galiano 1983), the small felid *Lynx* (MacFadden & Galiano 1981), and the wolverine *Plesiogulo* (Harrison

1981). Mammals restricted to latest Hemphillian (Hh4) faunas are the protoceratid *Kyptoceras* (Webb 1981), the horses *Astrohippus stockii*, *Dinohippus mexicanus*, and *Pseudhipparion simpsoni* (MacFadden 1986; Webb & Hulbert 1986), and the cervid *Eocoileus* (Webb 2000). Most Palmetto Fauna sites contain diverse marine vertebrate faunas and are located at about 50 m in elevation, indicating deposition during a period of high sea level in the early Pliocene (early Zanclean), shortly after the Messinian low sea level stand (5.3-7.1 Ma). Mammalian biochronology and sea-level data constrain the age of the Palmetto Fauna to the latest Hemphillian between 4.9 and 5.3 Ma.

BLANCAN

Macaspphalt Shell Pit.—The Macaspphalt Shell Pit LF (Fig. 2, site 8) was collected from a commercial shell mine located near Sarasota in Sarasota County in southwestern Florida, less than 10 km inland from the Gulf of Mexico (Hulbert 1987; Morgan & Ridgway 1987; Jones et al. 1991; Emslie 1992; Morgan & Hulbert 1995). Most of the fauna was recovered by FLMNH field crews in the mid 1980s. This mine is also known as the Warren Brothers Pit and APAC Mine. The site no longer exists as the shell pit was allowed to fill with water and is now part of a housing development. The Macaspphalt Shell Pit vertebrate fauna consists of a mixture of nearshore marine, estuarine, freshwater, and terrestrial taxa derived from a dark organic layer up to 1 m thick. The vertebrate-bearing unit and the extensive Pliocene marine shell beds that occur both below and above it are referred to the Pinecrest Sand Member of the Tamiami Formation. The late Blancan vertebrate fauna consists of more than 100 species, including over 40 taxa of birds (Emslie 1992) and 25 species of mammals (Morgan & Hulbert 1995). Five members of the Interchange fauna are known from Macaspphalt (Table 1). Other characteristic Blancan mammals present are the large mustelid *Trigonictis macrodon*, the three-toed horses *Nannippus peninsulatus* and *Cormohipparion emsliei* (type locality), the peccaries *Mylohyus floridanus* and *Platygonus bicalcaratus*, the camelid *Hemiauchenia blancoensis*, the gomphotheriid proboscidean *Rhynchotherium falconeri*, the leporid *Sylvilagus webbi*, the pocket gopher *Geomys* (= *Orthogeomys* after Ruez 2001) *propineta*, and the extinct cotton rat *Sigmodon medius*. Prior to the discovery of *Cormohipparion* at Macaspphalt, this hipparionine equid genus was thought to have gone extinct at the end of the Hemphillian (Hulbert 1987). In the southwestern United

States, South American immigrants first appeared about 2.7 Ma (Galusha et al. 1984), and *Nannippus* and *Rhynchotherium* are unknown in sites younger than 2.2 Ma (Lindsay et al. 1984). Therefore, biostratigraphic data suggest an age range of 2.2-2.7 Ma for the Macaspphalt Shell Pit LF based on the co-occurrence of *Nannippus*, *Rhynchotherium*, and numerous other typical Blancan mammals with four genera of South American immigrants that first appeared in the late Blancan (Fig. 1).

The Macaspphalt Shell Pit LF is one of the few Florida Interchange faunas that has associated geochronologic data, including paleomagnetic stratigraphy, strontium isotope chronostratigraphy, and sea level data. Strata from the vertebrate-bearing layer and all overlying units at the Macaspphalt Shell Pit have a reversed magnetic signature (Jones et al. 1991), indicating referral to the lower Matuyama Chron (2.15-2.58 Ma). The combination of paleomagnetic stratigraphy and biostratigraphy constrains the age of the Macaspphalt Shell Pit LF between 2.2 and 2.6 Ma. Evidence from strontium isotopes and ostracode biostratigraphy further supports this age range for the Macaspphalt vertebrate fauna (Jones et al. 1991). The presence of terrestrial vertebrates in a predominantly marine section suggests that the Macaspphalt Shell Pit LF may have been deposited during the regressive event associated with the onset of continental glaciation in the Northern Hemisphere at about 2.4 Ma (Shackleton et al. 1984).

Kissimmee River.—The Kissimmee River LF is derived from several sites along the Kissimmee River south of Ft. Basinger in Okeechobee County in southern peninsular Florida (Fig. 2, site 9). Vertebrate fossils were collected from the Kissimmee River basin in the late 1960s and early 1970s, mostly by Howard Converse, as a result of a project by the U. S. Army Corps of Engineers to channelize the Kissimmee River. The spoil piles created by the dredging of the river channel produced an extensive Pliocene marine molluscan fauna typical of the Pinecrest Sand Member of the Tamiami Formation, as well as a diverse late Blancan vertebrate fauna (Morgan & Hulbert 1995). Although the Kissimmee River LF was collected primarily from spoil piles and lacks direct stratigraphic context, it represents a uniform late Blancan assemblage that compares well to other Florida vertebrate faunas of this age, particularly the Macaspphalt Shell Pit LF. The close association of this fauna with the Pinecrest marine molluscan fauna is similar to the situation encountered at Macaspphalt and other late Blancan vertebrate sites from southern Florida,

including St. Petersburg Times, Brighton Canal, Lehigh Acres, and Acline Shell Pit (Morgan & Ridgway 1987; Morgan & Hulbert 1995). Like Macasphalt, the Kissimmee River LF consists of nearshore marine, freshwater, and terrestrial taxa, suggesting that the site formed in a shallow marine depositional environment. The surface elevation of about 10 m in the Kissimmee River area indicates this fauna was deposited during a period of high sea level, whereas the Macasphalt Shell Pit LF formed near modern sea level. Thus, sea level data suggest these two faunas are slightly different in age.

The Kissimmee River LF is composed of 24 species of mammals, including eight members of the Interchange fauna (Table 1). It is the oldest Florida record of *Pachyarmatherium*, better known from early Irvingtonian sites such as Leisey Shell Pit and Haile 16A (Downing & White 1995). Kissimmee River is one of the earliest North American records of *Eremotherium*, along with Brighton Canal and Lehigh Acres. Other characteristic Blancan mammals are *Nannippus peninsulatus*, *Platygonus bicalcaratus*, and the small antilocaprid *Capromeryx arizonensis*. Kissimmee has one of the earliest Florida records of the short-faced bear *Arctodus pristinus* (Emslie 1995b). The association of a diverse Interchange fauna with *Nannippus peninsulatus* places the age of the Kissimmee River LF between 2.2 and 2.7 Ma.

Haile 15A.—The Haile 15A site is from the Haile Quarry complex about 5 km northeast of Newberry, Alachua County, Florida (Fig. 2, site 13). This site was excavated by FSM field crews in the mid 1960s and has since been destroyed by mining operations. The Haile 15A LF was derived from undifferentiated sands and clays filling a karst fissure developed in marine Eocene limestone of the Crystal River Formation (Robertson 1976). Among the 23 species of mammals identified from Haile 15A (Robertson 1976) are four Interchange taxa: *Dasybus bellus*, *Holmesina floridanus* (type locality), *Glossotherium chapadmalense*, and *Hydrochaeris holmesi*. Robertson (1976) noted the close similarity between two of the Interchange mammals from Haile 15A, *H. floridanus* (originally referred to the South American genus *Kraglievichia*) and *G. chapadmalense*, to Pliocene taxa from Argentina. This is the earliest record of *Hydrochaeris holmesi* (Ahearn 1981). Most other late Blancan capybara records from Florida are *Nechoerus dichroplax* (Ahearn & Lance 1980; Ahearn 1981; Morgan & Hulbert 1995). The discovery of South American Interchange mammals at Haile 15A had a major influence on Dave Webb's early

work on the GABI (e.g., Webb 1976). Other diagnostic Blancan mammals include (Robertson 1976; Morgan & Hulbert 1995): the otter *Satherium piscinarium*, *Orthogeomys propineta*, *Sigmodon medius*, the horses *Nannippus peninsulatus* and *Equus simplicidens*, and *Mylohyus floridanus* (type locality). Haile 15A documents late occurrences of two species known from the latest Hemphillian Palmetto Fauna in central Florida, the flying squirrel *Cryptopterus* (= *Miopetaurista*) *webbi* (type locality) and *Cormohipparion emsliei*, originally described from the Macasphalt Shell Pit, but best known from the late Hemphillian Palmetto Fauna (Hulbert 1987). The co-occurrence of *Nannippus* with *Dasybus*, *Holmesina*, *Glossotherium*, and *Hydrochaeris* constrains the age of Haile 15A between 2.2 and 2.7 Ma.

Because Haile 15A was deposited in an isolated paleokarst deposit, only limited geochronologic data are available, including biochronology and data from sea level. This site is located about 80 km inland from the Gulf of Mexico and about 30 m above present sea level. The vertebrate fauna contains a large sample of nearshore marine fishes, which led Robertson (1976) to propose deposition during a period of high sea level. Evidence from eustatic sea level curves (Haq et al. 1987) and oxygen isotopes (Shackleton & Opdyke 1977; Shackleton et al. 1984) indicates a period of low sea level between 2.2 and 2.7 Ma; however, there were also periods of higher sea level at 2.1 and 2.3 Ma (Shackleton & Opdyke 1977). The high sea level stand at about 2.3 Ma best approximates the age of Haile 15A, as the presence of *Nannippus* indicates an age older than 2.2 Ma.

Santa Fe River 1.—Vertebrate fossils have been collected from river-bottom deposits along a 10 km segment of the Santa Fe River in northern peninsular Florida. The Santa Fe River 1 LF (Fig. 2, site 14), including sites 1, 1A, and 1B, was collected by FSM crews in the 1960s and again by FLMNH crews in the mid 1990s, from a bend in the river less than 0.5 km in length. This region of the Santa Fe River produces a mixture of Blancan and Rancholabrean vertebrates; however, these assemblages can be readily separated because there is virtually no overlap in their mammalian faunas. This mixture of late Pliocene and late Pleistocene faunas has caused some confusion in the past because this site was originally thought to be a pure, in-place Blancan vertebrate assemblage (Webb 1974). Although Santa Fe River 1B does have a high proportion of Blancan vertebrates, there apparently was some reworking of this deposit in the late Pleistocene with the subsequent admixture of Rancholabrean taxa (Morgan & Hulbert 1995), includ-

ing *Didelphis virginiana*, *Megalonyx jeffersonii*, *Holmesina septentrionalis*, *Castoroides ohioensis*, *Mammuthus columbi*, and *Trichechus manatus*. Conversely, the giant flightless bird *Titanis walleri* was originally described from Santa Fe River 1 as Pleistocene in age (Brodkorb 1963), but is now known to be restricted to late Pliocene faunas in Florida.

The Santa Fe River 1 LF has a diverse assemblage of South American immigrants consisting of six species (Table 1). Santa Fe River 1 is the type locality of *Titanis walleri* and has the largest sample of this species (Brodkorb 1963; Chandler 1994; Gould and Quitmyer this volume). This site also has one of the largest samples of *Glyptotherium arizonae* known from Florida. The Santa Fe River is one of four Florida late Blancan sites, also including Brighton Canal, Kissimmee River, and St. Petersburg Times, in which *G. arizonae* co-occurs with *Nannippus*. Other characteristic Blancan mammals from Santa Fe River 1 include: the borophagine dog *Borophagus diversidens*, the coyote-like dog *Canis lepophagus*, *Trigonictis macrodon*, the hyena *Chasmaporthetes ossifragus*, *Nannippus peninsulatus*, *Platygonus bicalcaratus*, *Capromeryx arizonensis*, and *Rhynchotherium*. The association of *Borophagus*, *Nannippus*, and *Rhynchotherium* with a diverse suite of South American immigrants constrains the age of the Santa Fe River 1 LF to the early late Blancan (2.2-2.7 Ma).

Haile 7C.—The Haile 7C LF was derived from a solution feature in the Haile Quarry complex, 5 km northeast of Newberry in Alachua County, northern Florida (Fig. 2, site 15). The Haile 7C site was worked from 1988 to 2000 by field crews from the FLMNH. Undifferentiated clays and sands were deposited in what appears to have been a water-filled sinkhole, developed in the marine Eocene Crystal River Formation. The vertebrate assemblage is particularly rich in freshwater species such as *Alligator* and the turtles *Trachemys platymarginata* and a large undescribed species of *Chelydra*, as well as mammals often associated with freshwater deposits, such as *Eremotherium* and *Tapirus*. The most notable features of Haile 7C are the abundance of complete turtle shells, many with skulls and postcranial skeletons, and numerous partial to complete skeletons of *Eremotherium* and *Tapirus*. Haile 7C has seven species of South American immigrant mammals (Table 1). Haile 7C represents the earliest record of *Erethizon* from Florida (Hulbert 1997). While slightly older specimens of *Eremotherium* are known from Kissimmee River, Brighton Canal, and Lehigh Acres in

southern Florida; however, Haile 7C has by far the largest sample of *E. eomigrans*.

The precise age of Haile 7C is difficult to determine because it lacks both typical Blancan mammals (*Borophagus*, *Nannippus*, *Rhynchotherium*) and typical Irvingtonian mammals (*Mammuthus*, *Palaeolama*, *Nothrotheriops*). Although Haile 7C is located less than 1 km from Haile 15A, the vertebrate faunas from these sites are quite different. Haile 7C not only lacks the diagnostic Blancan mammals found at Haile 15A, but also lacks marine vertebrates, indicating that Haile 7C was not deposited during a high sea level stand. The most convincing age data comes from the stage of evolution of *Holmesina floridanus*. Hulbert and Morgan (1993) studied samples of *Holmesina* from late Blancan and Irvingtonian sites in Florida and demonstrated that this genus underwent a rapid size increase between the late Blancan and early Irvingtonian (1.5-2.7 Ma). The sample of *H. floridanus* from Haile 7C, including a partial carapace, a complete skull, and a postcranial skeleton, is intermediate in size between *H. floridanus* samples from early late Blancan sites (Haile 15A, Macasphalt Shell Pit) and latest Blancan sites (Inglis 1A, De Soto Shell Pit). The two most abundant turtles, *Trachemys platymarginata* and a new *Chelydra*, are found at Haile 15A, but differ from the turtles at Inglis 1A and De Soto Shell Pit. The stage of evolution of *H. floridanus* and the turtle fauna suggests that Haile 7C is latest Blancan (2.0-2.2 Ma), slightly younger than early late Blancan sites that contain *Nannippus*, and slightly older than very latest Blancan sites (Morgan & Hulbert 1995; Hulbert 1997).

Inglis 1A.—The Inglis 1A LF was derived from a karst solution feature in the bank of the now-defunct Cross-Florida Barge Canal, near Inglis in Citrus County in northern Florida, about 7 km inland from the Gulf of Mexico (Fig. 2, site 16). Inglis 1A consists of layers of clay and sand filling a sinkhole/cave system formed in marine Eocene limestone of the Inglis Formation. This site was discovered in the late 1960s (Klein 1971) and worked by FSM field crews until 1974 (Webb 1974). A portion of the deposit was removed from the sinkhole by a dredge and wet screened to recover the fossils. Inglis 1A has an extremely diverse vertebrate fauna numbering over 150 species, including 53 species of mammals (Webb & Wilkins 1984; Morgan & Hulbert 1995), 47 species of birds (Emslie, 1998), and 31 species of squamate reptiles consisting of 26 snakes, four lizards, and one amphisbaenian (Meylan, 1982), as well as large samples of amphibians (Meylan this volume) and turtles.

Most previous authors placed Inglis 1A in the earliest Irvingtonian (Webb 1976; Webb & Wilkins 1984; Morgan & Hulbert 1995); however, evidence presented below suggests this site is latest Blancan. Inglis 1A has the second richest Interchange fauna of any site in North America with a total of ten species (Table 1). This is one of the few late Blancan records of *Paramylodon harlani*, better known from the Irvingtonian and Rancholabrean (McDonald 1995). Most other Florida late Blancan mylodont records are the smaller species *Glossotherium chapadmalense* (Table 1). Inglis 1A is the only late Blancan record for the extinct vampire bat *Desmodus archaeodaptes* (Morgan et al. 1988). This site also has the oldest record of *Erethizon kleini*, otherwise known only from Merritt Island along the Atlantic Coast (Frazier 1981).

Morgan and Hulbert (1995) concluded, as had most previous workers, that Inglis 1A is very early Irvingtonian in age (1.8-2.0 Ma). This numerical age is still accurate, but the absence of taxa characteristic of the Irvingtonian NALMA (e.g., *Mammuthus*, *Microtus*, *Nothrotheriops*, *Palaeolama*) strongly indicates a latest Blancan age. Inglis 1A lacks many of the mammalian genera considered classic Blancan indicators (*Borophagus*, *Hypolagus*, *Nannippus*, *Rhynchotherium*), but does have other taxa that are characteristic of Blancan faunas (*Megalonyx leptostomus*, *Chasmaporthetes ossifragus*, *Trigonictis macrodon*, *Capromeryx arizonensis*). Two species of small mammals described from Inglis 1A, *Sylvilagus webbi* (White 1991b) and *Orthogeomys propineticus* (Wilkins 1984; Ruez 2001), are known from the late Blancan Macaspalt Shell Pit LF, as well as the earliest Irvingtonian Haile 16A LF. This site also has a second leporid, a large and possibly undescribed species of the jackrabbit *Lepus* (Morgan & Hulbert 1995). The earliest records of *Lepus* are from two western latest Blancan sites, the Borchers LF in Kansas and the Anza-Borrego Desert in southern California (White 1991a). The only microtine rodent from Inglis, the extinct muskrat *Ondatra idahoensis* (Morgan & White 1995), is typical of late Blancan faunas such as the type locality, the Grand View LF from Idaho (Repenning 1987). The diverse vertebrate fauna from Inglis 1A is so abundantly sampled (thousands of specimens representing over 150 species) that the absence of diagnostic Irvingtonian taxa is almost certainly significant, and indicative of a latest Blancan age (1.8-2.0 Ma). The Curtis Ranch Fauna from the San Pedro Valley in Arizona (Johnson et al. 1975; Lindsay et al. 1990) is closely correlative with Inglis 1A (Fig. 1). Age-

diagnostic mammals shared by Curtis Ranch and Inglis 1A include *Glyptotherium arizonae*, *Canis edwardii*, *Sigmodon curtisi*, *Ondatra idahoensis*, and *Capromeryx arizonensis*. Curtis Ranch was long considered very early Irvingtonian as well (Johnson et al. 1975; Repenning 1987); however, Lindsay et al. (1990) referred this site to the late Blancan because it lacks genera that characterize the Irvingtonian.

The Inglis 1A site was deposited as much as 5 m below current sea level. Despite its low elevation, Inglis 1A totally lacks marine species suggesting that the site was deposited during a glacial period characterized by low sea level. Richmond and Fullerton (1986) recorded a glacial interval between 1.87 and 2.01 Ma (corresponding with marine isotope stage 40), an age in close agreement with the Inglis mammalian biochronology. Correlation of Inglis 1A with a glacial interval is also supported by the presence of certain species of reptiles, birds, and mammals that suggest cooler and/or more arid conditions (Meylan 1982; Webb & Wilkins 1984; Morgan 1991; Emslie 1998).

Inglis 1C.—The Inglis 1C site is also located along the Cross-Florida Barge Canal near Inglis in Citrus County, Florida, about 1 km east of the better known Inglis 1A locality (Fig. 2, site 17). The site consists of alternating layers of sand and clay deposited in a small sinkhole formed in the marine Eocene Inglis Formation. Inglis 1C was discovered and excavated in the mid 1990s. Emslie (1998) reviewed the avifauna and Ruez (2001) described the rodents and provided a mammalian faunal list consisting of 33 species. Inglis 1C has a limited Interchange fauna (Table 1). Furthermore, the fauna lacks most of the characteristic Blancan taxa present at Inglis 1A and contains *Palaeolama* which Morgan and Hulbert (1995) suggested did not appear until the early Irvingtonian. Emslie (1998) and Ruez (2001) placed Inglis 1C in the very early Irvingtonian; however, both authors were influenced by previous age assignments of the Inglis 1A LF (Morgan & Hulbert 1995). Inglis 1C is also located near modern sea level and lacks marine vertebrates, indicating deposition during a glacial interval. Inglis 1A and 1C probably were not deposited during the same glacial interval based on their difference in age.

Ruez (2001) noted that Inglis 1C and Inglis 1A are similar in age based on the joint occurrence of five species of extinct rodents: *Ondatra idahoensis*, *Orthogeomys propineticus*, *Peromyscus sarmocophinus*, *Reithrodontomys wetmorei* and *Sigmodon curtisi*, and the extinct rabbit *Sylvilagus webbi*. *Ondatra idahoensis* is primarily restricted to late Blancan fau-

nas (Repenning 1987). The two Inglis sites share *S. curtisi* with two other latest Blancan sites, De Soto Shell Pit and Curtis Ranch Fauna in Arizona (type locality). An extinct genus and species of microtine rodent, *Atopomys texensis*, occurs in Inglis 1C, De Soto Shell Pit, and Haile 16A, but not Inglis 1A. Despite the overall similarities in the small mammal faunas of the two Inglis sites, the absence of *Chasmaporthetes*, *Trigonictis*, and *Capromeryx* from Inglis 1C and the presence of *Palaeolama* suggest a slightly younger age than Inglis 1A. Inglis 1C is tentatively regarded as very latest Blancan in age (~1.8 Ma).

De Soto Shell Pit.—The De Soto Shell Pit LF was collected from several commercial shell mines south of Arcadia in De Soto County in southern peninsular Florida (Fig. 2, site 18). The vertebrate fauna was derived from organic sands and clays that occur within the extremely fossiliferous marine shell beds of the Pliocene Caloosahatchee Formation. Despite being separated by over 200 km and occurring in totally different depositional environments, the De Soto Shell Pit and Inglis 1A mammalian faunas are remarkably similar. Of the 32 species of mammals from De Soto, 25 species also occur at Inglis 1A. The entire Interchange fauna from the De Soto Shell Pit is also found at Inglis 1A (Table 1). Other diagnostic Blancan mammals shared by De Soto Shell Pit and Inglis 1A are: *Chasmaporthetes ossifragus*, *Trigonictis macrodon*, *Ondatra idahoensis*, and *Capromeryx arizonensis*. Mammals characteristic of Florida latest Blancan and/or earliest Irvingtonian faunas that occur in these two sites include: *Canis edwardii*, *Orthogeomys propineta*, *Sigmodon curtisi*, *Sylvilagus webbi*, and a newly described species of small lamine camelid *Hemiauchenia gracilis* (Meachen this volume). De Soto also has yielded two characteristic Blancan mammals not present in Inglis 1A, the otter *Satherium piscinarium* (also known from Haile 15A) and the diminutive cotton rat *Sigmodon minor*. The similarity between the mammalian faunas from De Soto Shell Pit and Inglis 1A confirms that these two sites are close in age (latest Blancan, 1.8-2.0 Ma). De Soto Shell Pit shares five species of age-diagnostic small mammals with Inglis 1C: *Atopomys texensis*, *Ondatra idahoensis*, *Orthogeomys propineta*, *Sigmodon curtisi*, and *Sylvilagus webbi*. However, the presence of *Chasmaporthetes*, *Trigonictis*, *Satherium*, and *Capromeryx* at De Soto Shell Pit, and their absence from Inglis 1C, indicates a somewhat older age for the former site.

The principal difference between the De Soto Shell Pit and Inglis 1A faunas is the diverse assemblage of

marine vertebrates from De Soto, including sharks, bony fishes, and the monk seal *Monachus*. The De Soto Shell Pit site was deposited during an interglacial interval when sea level was 5-10 m higher than present, whereas Inglis 1A formed during a glacial interval when sea level was at least 5 m lower. Based on the oxygen isotope record, there was a high sea level stand at about the time of the Pliocene/Pleistocene boundary at 1.8 Ma (Shackleton & Opdyke 1977). Other evidence for the age of the De Soto Shell Pit LF comes from the diverse marine molluscan fauna of the Caloosahatchee Formation, derived from marine shell beds in direct stratigraphic superposition both below and above the unit that produced the terrestrial mammals. Lyons (1991) considered the molluscan fauna of the Caloosahatchee Formation to be late Pliocene in age (older than 1.8 Ma). Corals collected near the top of the Caloosahatchee Formation have yielded Helium/Uranium dates of 1.78-1.89 Ma (Bender 1973). These dates and the biostratigraphy of the marine mollusks are consistent with the latest Blancan age (1.8-2.0 Ma) for the De Soto Shell Pit LF suggested by the mammalian biochronology.

IRVINGTONIAN

Haile 16 A.—The Haile 16A LF is located in the Haile Quarry complex about 5 km northeast of Newberry, Alachua County, northern Florida (Fig. 2, site 20). The fossils were derived from massive, dark, silty clays filling a fissure developed in marine Eocene limestone of the Crystal River Formation. The areal extent, depth, and stratigraphy of this site are unknown because the deposit was destroyed by mining operations before it could be carefully excavated. Ironically, the same limestone mining operations that are responsible for the initial discovery of most of the Haile sites eventually lead to their destruction. The vertebrate fauna from Haile 16A was collected by FSM field crews in the early 1970s by surface collecting and screenwashing spoil piles left after the fissure was mined out. Despite the lack of stratigraphic control, there is no indication that the fauna is mixed. Haile 16A has an unusual large mammal fauna that is dominated by the ground sloths *Megalonyx*, *Eremotherium*, and *Paramylodon*, and the short-faced bear *Arctodus pristinus*. Ungulates are uncommon and proboscideans are absent. The microvertebrate fauna is abundant and diverse. The mammalian fauna consists of 33 species, including eight members of the Interchange fauna (Table 2; Morgan & Hulbert 1995). Haile 16A has a large sample of *Pachyarmatherium leiseyi*, including several hundred osteoderms and a few isolated postcranial elements (Downing & White 1995).

The *Holmesina* from Haile 16A is similar in size to *H. floridanus* from the latest Blancan Inglis 1A LF and early Irvingtonian Leisey Shell Pit LF (Hulbert & Morgan 1993). Haile 16A has the Irvingtonian species of *Megalonyx*, *M. wheatleyi*, whereas the smaller *M. leptostomus* occurs in Florida late Blancan sites (McDonald 1977; Morgan & Hulbert 1995). There is a significant sample of *Eretherium eomigrans* (De Iuliis & Cartelle 1999). Morgan et al. (1988) referred two partial limb bones from Haile 16A to the vampire bat *Desmodus archaeadaptus*. Haile 16A is the oldest known record of the extant porcupine *Erethizon dorsatum* (Frazier 1981).

Haile 16A was long considered medial Irvingtonian (Frazier 1981; Morgan et al. 1988; Morgan 1991), but Morgan and Hulbert (1995) strongly advocated an early Irvingtonian age for this fauna. Bell et al. (2004) considered Haile 16A to be late Blancan; however, their placement of the Blancan/Irvingtonian boundary (1.35 Ma) is younger than the boundary recognized here (~1.6 Ma). Haile 16A lacks *Mammuthus*, the most characteristic Irvingtonian indicator, but proboscideans are absent from this fauna and are notably rare in Florida Pliocene-Pleistocene karst deposits. Morgan and Hulbert (1995) suggested that the short-limbed llama *Palaeolama*, which occurs at Haile 16A, may have its first appearance at the beginning of the Irvingtonian. Ruez (2001) also identified *Palaeolama* from Inglis 1C, a site that may be an earliest Irvingtonian correlative of Haile 16A. Martin (1995) described the new species *Microtus (Pedomys) australis* from the Haile 16A LF, with referred material from Leisey Shell Pit (Morgan & White 1995). Haile 16A and Leisey Shell Pit probably represent two of the earliest North American records of *Microtus*, which occurs in early Irvingtonian faunas but is absent from the late Blancan. Haile 16A and Leisey Shell Pit share the following species, all of which are absent from Florida latest Blancan faunas (e.g., Inglis 1A and De Soto Shell Pit): *Megalonyx wheatleyi*, *Erethizon dorsatum*, *Sigmodon libitinus*, *Microtus australis*, and *Palaeolama mirifica*. The occurrence of these species at Haile 16A, in particular *Microtus australis* and *Palaeolama mirifica*, suggests this fauna is very early Irvingtonian in age. However, several mammals from Haile 16A are more typical of late Blancan faunas: *Trigonictis cookii* (Ray et al. 1981); *Orthogeomys propinetus*; and *Sylvilagus webbi*. All western records of *Trigonictis* are Blancan, which suggests that Haile 16A is either the only Irvingtonian record of this genus or that this site is very latest Blancan. The arvicoline

rodent *Atopomys texensis* occurs at Haile 16A, Inglis 1C, and De Soto Shell Pit (Winkler & Grady 1990; Morgan & Hulbert 1995; Ruez 2001). The Haile 16A LF must be close in age to the Blancan/Irvingtonian boundary as defined here (~1.6 Ma), slightly younger than Inglis 1C and slightly older than Leisey Shell Pit (Fig. 1).

Leisey Shell Pit.—The Leisey Shell Pit LF was collected from two adjacent commercial shell mines located 7 km southwest of Ruskin and less than 1 km inland from Tampa Bay in Hillsborough County, southwestern Florida (Hulbert & Morgan 1989; Webb et al. 1989; Morgan & Hulbert 1995; Fig. 2, site 21). Leisey Shell Pit is probably the richest (tens of thousands of fossils), most diverse (203 species), and thoroughly studied Irvingtonian vertebrate fauna in North America (Hulbert et al. 1995). The vertebrate fauna was collected between 1983 and 1987 by the FLMNH and large volunteer field crews from two in-place quarry samples (Leisey Shell Pit 1A and Leisey Shell Pit 3A) that occurred in thin layers (less than 1 m thick) within marine shell beds of the Bermont Formation.

Leisey Shell Pit has the largest Interchange vertebrate fauna in North America, numbering 12 species (Table 2). Five of these are shared with the second richest Florida Interchange site, the latest Blancan Inglis 1A LF, whereas the remaining seven species are either absent from Inglis 1A or are represented by the same genus but different species (Tables 1-2). Paleogeological or biogeographic differences must account for the presence of *Aiolornis*, *Pachyarmatherium*, and *Neochoerus* at Leisey, but not Inglis 1A. All three genera are known from other late Blancan sites in Florida or the southwestern United States. The presence of *Nothrotheriops* at Leisey and its absence from Inglis 1A probably is related to the difference in age between the two sites, as this genus apparently did not reach temperate North America until the early Irvingtonian (Akersten & McDonald 1991; McDonald 1995). Leisey has a sample of the Irvingtonian species, *Nothrotheriops texanus* (McDonald 1995). The only other Florida record of *N. texanus* is from the Pool Branch LF in Polk County, central Florida (McDonald 1985), an early Irvingtonian correlative of Leisey. The species differences in *Megalonyx* and *Erethizon* between Inglis and Leisey reflect evolution within these two Interchange lineages.

The Leisey Shell Pit LF is Irvingtonian in age based on the presence of *Nothrotheriops*, *Castoroides*, *Microtus*, *Palaeolama*, and *Mammuthus*, all of which are unknown from the Blancan. Irvingtonian species from

Leisey include *Nothrotheriops texanus*, *Megalonyx wheatleyi*, *Canis armbrusteri*, *Sigmodon libitinus*, *Microtus australis*, *Ondatra annectens*, *Platygonus vetus*, and *Mammuthus haroldcooki*. Leisey has one of the largest known Irvingtonian samples of *Mammuthus* (Webb & Dudley 1995). Although originally referred to *Mammuthus hayi*, Webb (pers. comm.) now considers *M. haroldcooki* to be the valid name for the Leisey mammoth. The Leisey *Mammuthus* is similar to other early Irvingtonian mammoths referred to *M. haroldcooki* from the Holloman Gravel Pit in Oklahoma (Dalquest 1977) and Gilliland LF in Texas (Hibbard & Dalquest 1966), and to *Mammuthus imperator* from Tortugas Mountain in New Mexico (Lucas et al. 1999). *Microtus* (*Pedomys*) *australis* occurs in Leisey and Haile 16A, both representing early records of this genus (Martin 1995). The muskrat *Ondatra annectens*, typical of early and medial Irvingtonian faunas, occurs in Leisey (Morgan & White 1995). *Castoroides* apparently evolved from *Procastoroides* in North America in early Irvingtonian, with Leisey representing the earliest record of the genus. The species *C. leiseyorum* (type locality) occurs at Leisey and possibly two other early Irvingtonian sites from Florida, Apollo Beach and Crystal River Power Plant (Morgan & White 1995).

The Leisey Shell Pit LF is correlative with several other early Irvingtonian faunas in Florida, including Apollo Beach, Crystal River Power Plant, Haile 21A, Pool Branch, Payne Creek Mine, and Rigby Shell Pit (Table 2), as well the Gilliland LF in Texas and the Holloman LF in Oklahoma (Morgan & Hulbert 1995). Three Blancan species present at Haile 16A and absent from Leisey, *Sylvilagus webbi*, *Orthogeomys propineta*, and *Trigonictis cookii*, suggest that Leisey is slightly younger than Haile 16A. The medial Irvingtonian McLeod LF also shares many species with the Leisey Shell Pit LF, but is younger based on the presence of the larger and more advanced species of pampathere *Holmesina septentrionalis*, the jaguar *Panthera onca*, a more advanced *Smilodon gracilis*, and the extinct round-tailed muskrat *Neofiber leonardi* (Frazier 1977; Berta 1987; Hulbert & Morgan 1993; Seymour 1993).

Leisey Shell Pit is the only Florida Irvingtonian site that has extensive associated geochronologic data, including magnetostratigraphy and strontium isotope chronostratigraphy, as well as data from sea level (Webb et al. 1989; MacFadden 1995). All paleomagnetic samples taken throughout the 5 m thick stratigraphic section in the two shell pits that produced the Leisey Shell Pit LF are of reversed magnetic polarity

(MacFadden 1995), suggesting correlation with the long reversed interval in the upper Matuyama Chron between the top of the Olduvai Subchron of normal polarity (younger than 1.77 Ma) and the bottom of the Jaramillo Subchron of normal polarity (older than 1.07 Ma). The presence of *Mammuthus* confirms that the Leisey section is younger than the Olduvai, as all previous North American records of mammoth are younger than 1.6 Ma. The interval between 1.1 and 1.6 Ma was a warm period of normal to high sea level lacking major glacial episodes (Richmond & Fullerton 1986), which is consistent with data from the two Leisey sites indicating they were deposited close to or above current sea level. Most of the uppermost Matuyama, between the top of the Jaramillo (0.99 Ma) and the beginning of the Brunhes Chron (0.78 Ma), corresponds to a period of continental glaciation characterized by lower sea levels (Richmond & Fullerton 1986). Moreover, vertebrate sites from 0.8-1.0 Ma contain a medial Irvingtonian fauna, whereas Leisey is clearly early Irvingtonian. Age constraints from mammalian biochronology (early Irvingtonian, 1.0-1.6 Ma), magnetostratigraphy (upper Matuyama Chron, 1.07-1.77 Ma), strontium isotope chronostratigraphy (~1.5-1.8 Ma), and high sea level correlating to a long warm period in the early Pleistocene (1.0-1.6 Ma), indicate an age range for the Leisey Shell Pit LF of about 1.4-1.6 Ma.

Haile 21A.—Haile 21A is located in the Haile Quarry complex, 5 km northeast of Newberry, Alachua County, northern peninsular Florida (Fig. 2, site 27). This site was excavated by FSM field crews in the early 1980s, and was destroyed by mining operations several years after its discovery. Haile 21A consisted of clays, sands, and limestone breccias filling a karst solution cavity in the marine Eocene Crystal River Formation (Morgan et al. 1988; Morgan 1991; Morgan & Hulbert 1995). The mammalian fauna consists of 20 species, but is overwhelmingly dominated by the large peccary *Platygonus vetus* (Wright 1995). In contrast to most other Florida Irvingtonian sites, small mammals are uncommon at Haile 21A, with the exception of bats (Morgan 1991; Morgan & Hulbert 1995). Four species of Interchange mammals are known from Haile 21A (Table 2). Haile 21A is the type locality of the oldest vampire bat, *Desmodus archaeodaptes*, an extinct species restricted to the latest Blancan and early Irvingtonian in Florida (Morgan et al. 1988). Haile 21A is early Irvingtonian in age (1.0-1.6 Ma) based on the strong similarity of its mammalian fauna with that of the Leisey Shell Pit, in particular the presence of *Sigmodon libitinus* and the canids *Canis*

armbrusteri and *C. edwardii*. These two canids occur together only in early Irvingtonian sites such as Leisey (Berta 1995). Haile 21A is the type locality for the large sabercat *Xenosmilus hodsonae* (L. D. Martin et al. 2000), a species also known from Inglis 1A, Haile 16A, and Leisey Shell Pit.

McLeod.—The McLeod LF was recovered from the McLeod Limerock Mine about 3 km north of Williston, Levy County, Florida (Fig. 2, site 29). This site was excavated in 1941 by a Frick Laboratory field party led by Ted Galusha and was long ago destroyed by mining operations (Frazier 1977). The fossils were collected from a grayish clayey sand deposited in a solution feature in marine Eocene limestone. Morgan and Hulbert (1995) listed 14 species of mammals from the McLeod LF, although their list is almost certainly incomplete. Three species of Interchange mammals are known (Table 2). The presence of *Holmesina septentrionalis* is significant because Leisey Shell Pit and all other Florida early Irvingtonian faunas have the smaller species *H. floridanus*. *H. septentrionalis* is the typical pampathere in Florida late Irvingtonian and Rancholabrean faunas (Hulbert & Morgan 1993). *Megalonyx wheatleyi*, represented by a nearly complete skeleton from McLeod, is characteristic of Irvingtonian faunas (McDonald 1977, 2003). Specimens of the sabercat *Smilodon gracilis* from McLeod are larger and more advanced than fossils of this species from Leisey (Berta 1987, 1995), suggesting a somewhat younger age. *S. gracilis* is unknown from late Irvingtonian and younger faunas (Morgan & Hulbert 1995). Seymour (1993) reported a nearly complete skeleton of the jaguar *Panthera onca* from McLeod. The earliest North American records of *P. onca* are from four medial Irvingtonian sites, McLeod, Hamilton Cave in West Virginia, Port Kennedy Cave in Pennsylvania, and Cumberland Cave in Maryland (Seymour 1993). The extinct round-tailed muskrat *Neofiber leonardi* occurs at McLeod, but is restricted to late Irvingtonian faunas in the western United States (Frazier 1977). The cotton rat *Sigmodon bakeri* is otherwise known from late Irvingtonian and early Rancholabrean faunas in Florida (Martin 1974, 1979; Morgan & Hulbert 1995). *H. septentrionalis* and *P. onca* indicate a post-early Irvingtonian age, whereas *S. gracilis* indicates a prelate Irvingtonian age. The association of these taxa constrains the age of McLeod to medial Irvingtonian (0.6–1.0 Ma). The occurrence of *N. leonardi* and *S. bakeri*, elsewhere first known from the late Irvingtonian, further suggests that McLeod is late in the medial Irvingtonian (~0.6–0.8 Ma).

Coleman 2A.—Coleman 2A was collected from a commercial limestone mine near Coleman, Sumter County, in the north-central portion of the peninsula (Fig. 2, site 30). The fauna was derived from clays and sands filling a karst solution feature developed in Eocene marine limestone (Martin 1974). Ritchie (1980) reviewed the avifauna and Martin (1974) monographed the mammalian fauna, consisting of 38 species. Five species of Interchange mammals are known (Table 2). Coleman 2A represents one of only three Irvingtonian records of *Didelphis*, the other two are the late Irvingtonian Sebastian Canal LF from Indian River County on the Atlantic Coast of Florida (Morgan & Portell 1996) and the medial Irvingtonian Fyllan Cave in Texas (Winkler & Gose 2003). The occurrence of *Holmesina septentrionalis* at Coleman 2A is indicative of medial Irvingtonian and younger faunas. Three mammals from Coleman 2A clearly establish an Irvingtonian age, *Arctodus pristinus*, *Canis armbrusteri*, and the large peccary *Platygonus*, none of which are known from the Rancholabrean. The presence of several other mammals places Coleman 2A in the late Irvingtonian. The tapir is *Tapirus veroensis*, the small Rancholabrean species, whereas Florida early Irvingtonian faunas have the larger species *T. haysii* (Hulbert 1995). The Rancholabrean and extant species of round-tailed muskrat, *Neofiber alleni*, first appears at Coleman; the medial Irvingtonian McLeod LF has the extinct species *N. leonardi* (Martin 1974; Frazier 1977). The association of Irvingtonian species (*Arctodus pristinus*, *Canis armbrusteri*, *Platygonus vetus*) with typical Rancholabrean species (*Didelphis virginiana*, *Tapirus veroensis*, *Neofiber alleni*) supports Martin's (1974) placement of Coleman 2A in the latest Irvingtonian (~0.3–0.4 Ma).

FLORIDA INTERCHANGE VERTEBRATES

AVES

Titanis.—The giant flightless bird *Titanis* was one of the most spectacular participants in the GABI (see Gould & Quitmyer this volume). *Titanis* is the only North American member of the otherwise strictly South American family Phorusrhacidae, a group consisting of large flightless predators up to 2 m in height (Chandler 1994). *Titanis* appears to have been the latest surviving member of the Phorusrhacidae, as the last South American members of this group went extinct in the early Pliocene (Webb 1976, 1991; Marshall 1985). Brodkorb (1963) described *Titanis walleri* from the Santa Re River 1 site in northern Florida, and assigned a Pleistocene age

to the fauna. Further studies determined that Santa Fe River 1 is a mixed late Blancan and Rancholabrean assemblage, and that *Titanis* is a member of the late Blancan fauna (Webb 1974; Morgan & Hulbert 1995). Further confirmation of a late Blancan age for *Titanis* came with the discovery of a second sample of *T. walleri*, from the latest Blancan Inglis 1A LF in Florida (Webb 1976; Chandler 1994; Emslie 1998; Gould & Quitmyer this volume). The only other Florida Blancan record of *Titanis* is an isolated phalanx from a canal spoil bank in Port Charlotte near the Gulf Coast in southwestern Florida (Chandler 1994; Emslie 1998). The Port Charlotte *Titanis* occurs with *Nannippus* (MacFadden & Waldrop 1980), indicating an age similar to Santa Fe River 1.

Baskin (1995) reported a phalanx of *Titanis* from a site on the Gulf Coastal Plain in southern Texas that contains a mixed assemblage of late Hemphillian and Rancholabrean taxa. Baskin (1995) assigned a Rancholabrean age to the *Titanis* toe based on its similarity in preservation to the Pleistocene members of the fauna and the absence of Blancan mammals from this assemblage. The range of *Titanis* must have retracted southward into Middle America during the Irvingtonian and Rancholabrean, as there is no record of this genus from the extremely rich Florida Pleistocene record.

Teratornis.—Teratorns are giant extinct vulture-like birds of the family Teratornithidae, best known from the late Pleistocene Rancho la Brea tar pits in southern California. Although rare, teratorns are also known from several late Blancan and early Irvingtonian sites in California, Florida, and Mexico. Campbell et al. (1999; see below) transferred the largest North American teratorn, *Teratornis incredibilis*, to the new genus *Aiolornis*. Emslie (1995a) reported several associated postcranial elements of *Teratornis merriami* from the early Irvingtonian Leisey Shell Pit, although he later stated that the Leisey *Teratornis* may represent an undescribed species (Emslie 1998). *T. merriami* was originally described from Rancho la Brea, and is also known from four Rancholabrean sites in Florida, Bradenton, Cutler Hammock, Reddick 1A, and Seminole Field (Brodkorb 1964; Emslie 1998). The oldest known member of the Teratornithidae is *Argentavis magnificens* from the late Miocene of Argentina, one of the largest known flying birds (Campbell & Tonni 1980). The absence of teratorns in pre-Pliocene sites in North America and their presence in the late Miocene of Argentina suggests this group evolved in South America and migrated northward into North America in the Blancan (Campbell & Tonni 1981; Emslie 1995a).

Aiolornis.—Campbell et al. (1999) studied the largest teratorns in North America previously placed in the species *Teratornis incredibilis*, and reassigned them to the new genus *Aiolornis*. The type locality of *A. incredibilis* is a Rancholabrean cave site in Nevada, but all other referred specimens of this species are from Irvingtonian and Blancan sites (Emslie 1995a; Campbell et al. 1999). Emslie (1995a) tentatively referred a partial carpometacarpus from the Leisey Shell Pit to *A. incredibilis*. The oldest records of *A. incredibilis* are early Blancan (~3.7 Ma) fossils from the Anza-Borrego Desert in southern California and the Rancho Viejo fauna in Guanajuato, central Mexico (Campbell et al. 1999). The *Aiolornis* from Anza-Borrego represents one of two or possibly three pre-late Blancan records of the Interchange fauna from temperate North America, questioning the validity of including flying birds in the Interchange.

MAMMALIA, MARSUPIALIA, DIDELPHIDAE

Didelphis.—The opossum *Didelphis* is one of only three genera of Interchange mammals of South American origin that are still extant in temperate North America, the other two are the armadillo *Dasybus* and the porcupine *Erethizon*. *Didelphis* was the last of the mammalian genera involved in the GABI to reach temperate North America. The earliest North American record of the opossum is an isolated lower molar referred to *Didelphis* sp. from the medial Irvingtonian Fyllan Cave in central Texas (Winkler & Gose 2003). The earliest fossils referred to the living species *D. virginiana* are from two late Irvingtonian sites in Florida, Coleman 2A LF in the central region of the peninsula (Martin 1974) and the Sebastian Canal LF along the central Atlantic Coast (Morgan & Portell 1996). All other fossil records of *D. virginiana* are Rancholabrean, mostly from Florida and the southeastern United States (Kurtén & Anderson 1980). Gardner (1973) hypothesized that *D. virginiana* evolved from the Neotropical species *D. marsupialis* in Middle America during the Pleistocene, and then spread northward because of its ability to tolerate cooler climates. However, there is no pre-late Pleistocene fossil record of *Didelphis* in Middle America to establish the timing of its arrival there.

XENARTHRA, DASYPODIDAE

Dasybus.—The armadillo *Dasybus* includes the large extinct species *D. bellus* and the living nine-banded armadillo *D. novemcinctus*, as well as several other extant species from South America. *D. bellus* was origi-

nally described from the RanchoLabrean Seminole Field LF on the Gulf Coast of Florida (Simpson 1929a), and is common in Florida RanchoLabrean faunas (Webb 1974; Morgan & Hulbert 1995). The oldest well-dated sites containing *D. bellus* are early late Blancan (2.2-2.6 Ma), including the Macasphalt Shell Pit LF in Florida and the Big Springs LF in Nebraska (Voorhies, 1987).

Dasypus bellus occurs in seven late Blancan (Table 1) faunas and eight Irvingtonian (Table 2) faunas in Florida. Late Blancan and Irvingtonian samples of *D. bellus* appear to represent a chronocline, with a general increase in size from the Blancan to the RanchoLabrean (Robertson 1976; Downing & White 1995). Several large samples of *D. bellus* from Florida late Blancan and early Irvingtonian sites provide important information on the systematics and early evolution of this species. *D. bellus* is primarily known from Florida throughout the late Blancan and most of the Irvingtonian. The only pre-RanchoLabrean records of *D. bellus* from outside Florida are the late Blancan Big Springs LF in Nebraska (Voorhies, 1987), the medial Irvingtonian Fyllan Cave and Kitchen Door LFs in central Texas (Winkler and Gose, 2003), and the late Irvingtonian Slaton LF in the Texas Panhandle (Dalquest 1967). *D. bellus* is widespread in the eastern United States during the RanchoLabrean, with records from as far north as Iowa, Missouri, Illinois, and Indiana, and west to New Mexico (Kurtén & Anderson 1980).

Pachyarmatherium.—*Pachyarmatherium* is the most recently recognized member of the South American immigrant fauna. *Pachyarmatherium leiseyi* is a peculiar large, thick-shelled armadillo, first described from the early Irvingtonian Leisey Shell Pit LF in Florida (Downing & White 1995). *P. leiseyi* is also known from five other early Irvingtonian sites in Florida (Table 2), as well as three late Blancan sites (Table 1). *Pachyarmatherium* also occurs in the late Blancan Walrus Ditch site in South Carolina (Downing & White 1995; James Knight pers. comm.). *Pachyarmatherium* has a restricted geographic and chronologic distribution. This genus first appears in the early late Blancan, with the oldest records from the Kissimmee River and El Jobean Shell Pit in southern Florida and from the Walrus Ditch in South Carolina. It occurs in association with *Nannippus* at all three of these sites. The largest samples of *P. leiseyi* are from early Irvingtonian sites, including Leisey Shell Pit and Haile 16A. The youngest records of *Pachyarmatherium* are late early Irvingtonian in age (~1.0 Ma).

The small, thick osteoderms of *Pachyarmatherium*

are immediately recognizable. Nonetheless, for many years, osteoderms of *Pachyarmatherium* were confused with *Dasypus bellus* in the FLMNH collection, even though *Dasypus* has much thinner osteoderms that have a different figure pattern and has imbricating or moveable osteoderms. The total absence of imbricating osteoderms in large samples of *Pachyarmatherium* from Leisey Shell Pit 1A and Haile 16A was the clue that led me and several other paleontologists (Kevin Downing, Richard Hulbert, and Dave Webb) to conclude that this really was a new and completely different type of shelled xenarthran unrelated to *Dasypus*. A nearly complete carapace and postcranial skeleton of *Pachyarmatherium* of probable early Irvingtonian age was collected about 1990 from a shell pit near Punta Gorda in Charlotte County along Florida's southwestern Gulf Coast. Unfortunately, before this remarkable specimen could be properly studied, it was sold to a commercial fossil dealer who eventually resold it to a museum in Japan. On the basis of a brief examination of this specimen at the Tucson Gem and Mineral Show in February 1992, Downing and White (1995) concluded that *Pachyarmatherium* was most closely related to armadillos (superfamily Dasypodoidea). They based their conclusion on the presence of claws rather than hooves, free dorsal vertebrae, and a small and possibly edentulous dentary, all of which are unlike glyptodonts. *Pachyarmatherium* had anterior and posterior bucklers that imbricated with one another, but it lacked moveable bands between the bucklers and hence lacked imbricating osteoderms (Downing & White 1995). McKenna and Bell (1997) tentatively placed *Pachyarmatherium* in the subfamily Glyptatelinae of the family Glyptodontidae. Downing and White (1995) also noted the similarity in certain morphological characters of *Pachyarmatherium* to glyptateline glyptodonts (e.g., *Glyptatelus*) from South America. Only the discovery of additional material of *Pachyarmatherium* and further study of the Punta Gorda specimen will clarify the relationships of this enigmatic xenarthran. If fossils of such a distinctive animal could remain virtually unnoticed for almost 20 years in the FLMNH vertebrate paleontology collection, then it seems likely that other undiscovered members of the South American Interchange fauna may still await discovery, in the field or in a museum drawer.

XENARTHRA, PAMPATHERIIDAE

Holmesina.—The pampathere *Holmesina* was the most widespread and common genus of South American immigrant in Florida during the late Blancan and

early Irvingtonian. Two species of *Holmesina* are recognized from Florida: *H. floridanus* (originally described as *Kraglievichia floridanus*) occurs from the late Blancan through early Irvingtonian; and *H. septentrionalis* from the medial Irvingtonian through Rancholabrean (Robertson 1976; Edmund 1985a, 1987; Hulbert & Morgan 1993). *H. floridanus* is present in 12 late Blancan and nine early Irvingtonian sites in Florida, which includes virtually every Florida site during this time interval (Tables 1-2; Hulbert & Morgan 1993; Morgan & Hulbert 1995). The earliest well-dated Florida site containing *H. floridanus* is the early late Blancan Macaspah Shell Pit. *Holmesina* is unknown elsewhere in temperate North America during the late Blancan. Pampatheres from several early Blancan sites in central Mexico originally identified as either *Holmesina* or *Pampatherium*, are now referred to the otherwise South American genus *Plaina* (Carranza-Castañeda & Miller 2004). The only non-Florida record of *H. floridanus* is from the early Irvingtonian Gilliland LF in western Texas (Hibbard & Dalquest 1966). Most records of *Holmesina* from outside Florida represent the large species *H. septentrionalis*, and are from Rancholabrean sites in the southeastern United States and Texas (Kurtén & Anderson 1980).

The morphology, systematics, evolutionary history, distribution, and biochronology of *Holmesina* in Florida have been thoroughly reviewed over the past three decades (Webb 1974; Robertson 1976; Edmund 1985a, b, 1987; Hulbert & Morgan 1993; Morgan & Hulbert 1995). Webb (1974a) and Robertson (1976) first documented the presence of pre-Rancholabrean pampatheres in Florida. They demonstrated a significant chronocline in size from small pampatheres in the Blancan to intermediate-sized animals in the Irvingtonian to large individuals in the Rancholabrean. Robertson (1976) described the new species *Kraglievichia floridanus* from Haile 15A, with referred material from the Santa Fe River 1 and 2. Robertson noted the similarity of the Florida species to the late Pliocene pampathere *Kraglievichia paranensis* from Argentina. Edmund (1987) concluded that the entire Florida lineage, from the late Blancan through the Rancholabrean, should be placed in the genus *Holmesina*, originally proposed by Simpson (1930a) for the late Pleistocene species *H. septentrionalis*. McKenna and Bell (1997) placed *Holmesina* within *Pampatherium*, but most workers have not followed their synonymy. Both Robertson (1976) and Edmund (1987) compared Florida samples of the small late Blancan *H. floridanus* with the much larger species *H.*

septentrionalis from the Rancholabrean. Edmund (1987) also studied several samples of intermediate size and age from Florida Irvingtonian sites, in particular Inglis 1A (now regarded as latest Blancan). Hulbert and Morgan (1993) presented a quantitative and qualitative analysis of *Holmesina* in Florida, including large samples collected after the studies of Robertson (1976) and Edmund (1987). Hulbert and Morgan (1993) demonstrated that the most significant size change in Florida *Holmesina* occurred during the late Blancan, but the most important morphological changes occurred between the early and medial Irvingtonian. They placed the species boundary between *H. floridanus* and *H. septentrionalis* at the time of maximum morphological change (more than ten morphological characters distinguish these two species), assigning small and medium-sized individuals from the late Blancan and early Irvingtonian to *H. floridanus* and large individuals from the medial Irvingtonian through the Rancholabrean to *H. septentrionalis*. *H. floridanus* osteoderms from Florida sites can be fairly accurately dated on the basis of size (e.g., early late Blancan, latest Blancan, early Irvingtonian).

XENARTHRA, GLYPTODONTIDAE

Glyptotherium.—The only genus of glyptodont identified from temperate North America is *Glyptotherium*, recorded from sites in the southwestern United States and Florida ranging in age from late Blancan through late Rancholabrean. In their monograph on North American glyptodonts, Gillette and Ray (1981) recognized three species from temperate North America, with essentially one species representing each of the three Plio-Pleistocene NALMA: *G. texanum* from the late Blancan; *G. arizonae* from the early Irvingtonian, and *G. floridanum* from the Rancholabrean. Two additional species, *G. cylindricum* and *G. mexicanum*, are known from late Pleistocene sites in central Mexico. *Glyptotherium* is one of four genera of South American immigrants recorded from sites in the southwestern United States that predate the Gauss/Matuyama boundary, and are thus older than 2.6 Ma. Gillette and Ray (1981) identified Florida late Blancan glyptodonts as *G. arizonae*, in particular a large sample of osteoderms from Santa Fe River. They considered all southwestern sites containing *G. arizonae* to be early Irvingtonian, including Curtis Ranch in Arizona (type locality), Gilliland in Texas, and Holloman in Oklahoma.

The largest samples of Blancan and Irvingtonian glyptodonts are from western Texas and southeastern

Arizona (Gillette & Ray 1981). Very little additional *Glyptotherium* material has been described from Arizona and Texas over the past 20 years, whereas several new late Blancan and early Irvingtonian glyptodont records have been reported from Florida (Morgan & Hulbert 1995), New Mexico (Vanderhill 1986; Lucas et al. 1993; Morgan & Lucas 2000a, b, 2003), and Oklahoma (Czaplewski 2004). New discoveries in Florida, and further study and refinement of the ages of late Blancan and early Irvingtonian faunas in both Florida (Morgan & Hulbert 1995) and the southwestern United States (Lindsay et al. 1990; Morgan & Lucas 2003), have led to minor modifications in the biochronologic ranges of the two species of glyptodonts found during this time interval. *G. texanum* appears to be limited to faunas from the early part of the late Blancan (~2.2-2.7 Ma) in the southwestern United States, including the Blanco (type locality) and Cita Canyon LFs in Texas and 111 Ranch in Arizona (Gillette and Ray, 1981). *G. arizonae* co-occurs with *Nannippus* in four early late Blancan sites in Florida: Brighton Canal, Kissimmee River, St. Petersburg Times, and Santa Fe River 1. Thus, *G. arizonae* occurred in late Blancan sites in Florida at the same time *G. texanum* was found in the southwestern United States. There are no sites known where these two species co-occur (Gillette & Ray 1981). *G. arizonae* is also found in latest Blancan (1.8-2.2 Ma) and early Irvingtonian (1.0-1.8 Ma) faunas in both the southwestern United States and Florida. Several of these latest Blancan sites, in particular, Curtis Ranch and Inglis 1A, were considered early Irvingtonian by Gillette and Ray (1981) and most other workers (e.g. Repenning 1987; Morgan & Hulbert 1995). De Soto Shell Pit is another latest Blancan record of *G. arizonae* from Florida. *G. arizonae* was uncommon in Florida during the early Irvingtonian, with the only published record being a small sample of osteoderms from the Leisey Shell Pit LF (Downing & White 1995). Early Irvingtonian samples of *G. arizonae* are also known from Gilliland and Rock Creek in Texas and Holloman in Oklahoma (Gillette & Ray 1981), all of which are similar in age to Leisey. Glyptodonts are unknown from the southwestern United States after the early Irvingtonian, and do not occur in Florida during the medial to late Irvingtonian. Glyptodonts reappear in Florida in the Rancholabrean where the species *G. floridanum* is known from numerous sites in the Florida peninsula, as well as from Edisto Beach in South Carolina and about ten sites on the Gulf Coastal Plain of Texas (Holmes & Simpson 1931; Webb 1974; Gillette & Ray 1981).

XENARTHRA, MYLODONTIDAE

Thinobadistes.—Webb (1989) reviewed the taxonomy of *Thinobadistes*, an endemic North American genus of late Miocene lestodontine mylodont ground sloth. *Thinobadistes* is only distantly related to the mylodontine mylodont *Glossotherium* (see below) whose arrival in North America in the late Pliocene represents a separate immigration event. The type locality of the earliest North American mylodontid species, *Thinobadistes segnis*, is the early Hemphillian Mixson's Bone Bed in Florida (Hay 1919; Webb 1989). Frick Laboratory field crews recovered a large sample of *T. segnis* from Mixson's in the late 1930s and early 1940s, although several specimens of this sloth were collected from this site in the late 1800s, including the type astragalus (Leidy & Lucas 1896; Hay 1919). A composite mounted skeleton of *T. segnis* from Mixson's Bone Bed is on display at the Florida Museum of Natural History (Webb 1989:fig. 1; see also Ray this volume). *T. segnis* has been reported from only one other locality, McGehee Farm, represented by a partial lower fourth molariform tooth. Webb (1989) described a larger and younger species, *T. wetzeli*, based on an astragalus and several other postcranial elements from the late early Hemphillian (7.0-7.5 Ma) Withlacoochee River 4X LF in north-central Florida. *T. wetzeli* is known from two other correlative late early Hemphillian sites, including a juvenile palate with both caniniforms from the nearby Withlacoochee River 4A LF and a juvenile mandible and astragalus from the Box T LF in Texas (Webb 1989). Hulbert et al. (2002) tentatively referred several specimens to *T. wetzeli* from the slightly older early Hemphillian (~7-8 Ma) Tyner Farm LF in northern Florida. Several teeth of *Thinobadistes* from the early late Hemphillian (~6.8-7.0 Ma) Coffee Ranch LF in Texas appear to be the youngest record of the genus (Dalquest 1983; Webb 1989). Webb (1989) also mentioned two teeth of *Thinobadistes* from an unknown stratigraphic level in the Bone Valley Formation of central Florida. Although the majority of mammals from the Bone Valley Formation are derived from the latest Hemphillian Palmetto Fauna (Morgan 1994; Webb et al. in press), *Thinobadistes* is absent from in-place samples of the Palmetto Fauna and is probably derived from the slightly older early Hemphillian Four Corners Fauna known from several phosphate mines in the Bone Valley Formation (Hulbert et al. 2003). *Thinobadistes* apparently went extinct in the early part of the late Hemphillian (~6-7 Ma). Mylodontid sloths are unknown in temperate North America in the latest Hemphillian and early Blancan, and then reappear in the late Blancan with the arrival of

Glossotherium.

Glossotherium/Paramylodon.—The mylodontid ground sloths *Glossotherium* and *Paramylodon* are discussed together because the North American late Pliocene and Pleistocene representatives of these two genera are either congeneric or have an ancestor-descendant relationship. There are several nomenclatural problems associated with these two generic names (McDonald 1995). *Paramylodon* was first proposed for the species *P. nebrascensis* from the Pleistocene of Nebraska, now synonymized with *P. harlani*, the oldest available species name for a North American mylodont. *Glossotherium* was first proposed for the late Pleistocene South American species *G. robustum*, but several other species have been referred to this genus, including *harlani*. Although the name *G. harlani* is often used for the North American Pleistocene mylodontid (e.g., Kurtén & Anderson 1980), McDonald (1995) noted that there is no morphological basis for referring *harlani* to *Glossotherium*. I follow McDonald (1995, 2003) in using *Paramylodon harlani* for North American late Blancan, Irvingtonian, and Rancholabrean mylodontid sloths.

McDonald (1995) recommended retaining the name *Glossotherium* for the small late Blancan mylodontid from North America, *G. chapadmalense*, until a more detailed study is conducted to determine its relationships to *G. chapadmalense* from the Pliocene of Argentina and to *Paramylodon harlani* from North American Pleistocene sites. I follow McDonald (1995) in using *G. chapadmalense* for the small North American late Blancan mylodontid, with several qualifications. I suspect that the small Blancan mylodontid belongs in *Paramylodon* rather than *Glossotherium*, especially if it is demonstrated to have a close phylogenetic relationship with the younger North American mylodontids. It is also doubtful that the North American Blancan mylodontid is correctly placed in the South American Pliocene species *chapadmalense*, considering that most other members of the Interchange fauna belong to endemic North American species and many belong to endemic North American genera. If the North American Blancan mylodontid is eventually demonstrated to be specifically distinct from *G. chapadmalense*, then the name *G. garbanii* is available, having been proposed for a small Blancan mylodontid from Guanajuato in central Mexico (Montellano-Ballesteros & Carranza-Castañeda 1986). Of course, that is contingent upon whether *G. garbanii* and the small late Blancan species from temperate North America are conspecific, which has yet to be demonstrated.

Mylodontid ground sloths are rare in North American late Blancan sites, with most records consisting of isolated elements. Robertson (1976) first used the name *Glossotherium chapadmalense* for the small North American Blancan mylodont, based on an associated maxilla, dentary, and partial postcranial skeleton from the Haile 15A LF in northern Florida. The Haile 15A partial skeleton is the most complete published specimen of a Blancan mylodont from North America. Webb (1974a) and Robertson (1976) also reported *G. chapadmalense* from the late Blancan Santa Fe River 1 LF in Florida. Other Florida late Blancan records of *G. chapadmalense* include a juvenile mandible, isolated teeth, and a femur from the Macasphalt Shell Pit, teeth from the Kissimmee River, a tooth from Lehigh Acres, and an ungual phalanx from Acline Shell Pit (Morgan & Hulbert 1995). Blancan mylodont records outside of Florida mostly consist of fragmentary remains. However, there is a fairly complete skull from the latest Blancan Mesilla Basin Fauna B in southern New Mexico (Vanderhill 1986), one of the youngest records of *G. chapadmalense*. Tedford (1981) and Tomida (1987) mentioned a specimen of *G. chapadmalense*, apparently consisting of much of a skeleton most of which remains in a plaster jacket (R. White, pers. comm), from the 11 Mile Wash locality in the Duncan basin in southeastern Arizona.

Glossotherium was one of the first South American immigrants to reach temperate North America following the onset of the second major pulse of the GABI in the late Blancan. The earliest dated late Blancan records of *Glossotherium* in the southwestern United States are from the uppermost Gauss Chron (~2.7 Ma), including Donnelly Ranch, Colorado (Hager 1974), Cita Canyon, Texas (Lindsay et al. 1976), and Pearson Mesa, New Mexico (Tomida 1987; Morgan & Lucas 2000a). The earliest well-dated *Glossotherium* from Florida is from the Macasphalt Shell Pit, dating to the lower Matuyama Chron (2.14-2.58 Ma). Tomida (1987) correlated the 11 Mile Wash *Glossotherium* with the nearby Country Club Fauna from the Duncan Basin in Arizona, which he regarded as early Blancan in age (~3.5 Ma) based on the biostratigraphy of the small mammals. Further study of the 11 Mile Wash site is warranted before an early Blancan age is proposed for the first appearance of *Glossotherium* (and the onset of the Interchange) in temperate North America, although *Glossotherium* is known from the early Blancan of central Mexico (Carranza-Castañeda 2004; Flynn et al 2005).

Larger mylodontid sloths from the latest Blancan and early Irvingtonian of Florida, including specimens from Inglis 1A, Haile 16A, and Leisey Shell Pit, have been referred to *Paramylodon harlani*, the typical Pleistocene mylodont (McDonald 1995). A large sample of *P. harlani*, including several skulls, mandibles, and postcranial elements, was described from the early Irvingtonian Leisey Shell Pit LF (McDonald 1995). The Leisey sample is intermediate in size and morphological characters between late Blancan mylodonts referred to *Glossotherium chapadmalense* and larger specimens of *P. harlani* from the Rancholabrean, but is more similar to the late Pleistocene species (McDonald 1995). Other early Irvingtonian records of *P. harlani* are from Holloman in Oklahoma, Rock Creek and Gilliland in Texas, and Fish Creek-Vallecito Creek in California (McDonald, 1995). *P. harlani* was widespread throughout temperate North America in the late Irvingtonian and Rancholabrean (Kurtén & Anderson 1980; McDonald 2003).

XENARTHRA, MEGALONYCHIDAE

Pliometanastes.—The type locality of the earliest North American megalonychid ground sloth, *Pliometanastes protistus*, is the early Hemphillian McGehee Farm LF in Florida (Hirschfeld & Webb 1968). The type specimen of *P. protistus* is a partial skull, and the sample also includes numerous postcranial elements. Hirschfeld and Webb (1968) also referred an edentulous mandibular symphysis from the late early Hemphillian Withlacoochee River 4A LF to *P. protistus*. Additional material of *P. protistus* from Withlacoochee River 4A includes a dentary with teeth, humerus, calcaneum, and astragalus. There is also a partial associated skeleton of *P. protistus* from the late early Hemphillian Moss Acres LF (Lambert 1994). Comparable elements from Moss Acres and Withlacoochee River 4A are similar to the sample of *P. protistus* from McGehee Farm. Several teeth of *P. protistus* are known from the early Hemphillian Haile 19A LF. *Pliometanastes* inhabited Florida throughout the early Hemphillian (~7-9 Ma). There is a partial skeleton of *P. protistus* from the Siphon Canal LF, Stanislaus County, California (Hirschfeld 1981). Hirschfeld and Webb (1968) described a second species, *?Pliometanastes galushai* from the early Hemphillian of New Mexico. Other early Hemphillian records of *Pliometanastes* include Dunnellon in Florida, Box T in Texas, North Santa Clara Canyon in New Mexico, and Klipstein Ranch in California (Hirschfeld & Webb 1968). The oldest radioisotopically-dated ground

sloth in North America is the partial skeleton of *P. protistus* from the Siphon Canal LF, which was found just below a tuff K-Ar dated at 8.19 Ma (Hirschfeld 1981). The Florida earliest Hemphillian records of *Pliometanastes* from McGehee Farm and Haile 19A are probably somewhat older (8.5-9.0 Ma).

Megalonyx.—Webb and Perrigo (1985) noted the stratigraphic continuity between *Pliometanastes* in the early Hemphillian and *Megalonyx* in the late Hemphillian, and suggested that this “chronocline” strongly supported the derivation of *Megalonyx* from *Pliometanastes* in North America. *Megalonyx* and *Pliometanastes* do not co-occur; *Megalonyx* first appeared in the early late Hemphillian, after the extinction of *Pliometanastes* in the late early Hemphillian. Since *Megalonyx* apparently evolved in North America, it was not a participant in the GABI, but instead represents an autochthonous evolutionary event. *Megalonyx* is discussed here because its progenitor was ultimately of South American origin.

Megalonyx underwent an evolutionary sequence in North America from the late Hemphillian through the late Rancholabrean, with essentially one species per NALMA, each differing in size and other morphological characters (McDonald 1977). The earliest well documented record of *Megalonyx* is a mandible with a complete dentition referred to *Megalonyx curvidens* from the early late Hemphillian (6-7 Ma) ZX Bar LF in Nebraska (Hirschfeld & Webb 1968; Hirschfeld 1981). The oldest record of *Megalonyx* in Florida is from the latest Hemphillian (~5 Ma) Palmetto Fauna. The largest late Hemphillian sample of *Megalonyx* from Florida, referred to *M. curvidens*, occurs in the Whidden Creek LF (Webb et al. in press). A second late Hemphillian species, *Megalonyx mathisi*, was described based on a skull from Black Rascal Creek, Merced County, California (Hirschfeld & Webb 1968). This site is apparently correlative with the latest Hemphillian Pinole LF in Contra Costa County, California, which has a radioisotopic date of 5.3 Ma from the Pinole Tuff (Hirschfeld 1981).

The only recognized Blancan species of *Megalonyx*, *M. leptostomus*, with its type locality at Mt. Blanco, Texas, occurs in Pliocene sites throughout much of North America from Florida to Texas to California and north to Idaho and Washington (Hirschfeld & Webb 1968; McDonald 1977; Kurtén & Anderson 1980). Several Florida late Blancan samples of *Megalonyx*, including specimens from Macasphalt Shell Pit, Haile 7C, and Inglis 1A, have been referred to *M. leptostomus*, although the Florida animals are notably smaller than *M.*

leptostomus from western Blancan sites (McDonald 1977; Morgan & Hulbert 1995). The larger Irvingtonian species, *M. wheatleyi*, has its type locality at Port Kennedy Cave in Pennsylvania, and also occurs in several Florida Irvingtonian sites (Table 2; McDonald 1977, 2003). The largest species of *Megalonyx* is *Megalonyx jeffersonii* from the Rancholabrean, which ranged throughout North America as far north as Alaska and northern Canada and south to Mexico (McDonald 1977, 2003).

XENARTHRA, MEGATHERIIDAE

Eremotherium.—During the late Blancan and early Irvingtonian, the giant megatheriid ground sloth *Eremotherium* is known only from Florida. *Eremotherium* was somewhat more widespread in the southeastern United States during the Rancholabrean with records on the Atlantic Coastal Plain from Florida north to Georgia and South Carolina and west to the Gulf Coastal Plain of Texas (Kurtén & Anderson 1980). *Eremotherium* apparently was primarily tropical in its distribution. It is the only one of the four genera of Plio-Pleistocene North American ground sloths that occurred widely in tropical America, including both Middle and South America (Cartelle & De Iuliis 1995). There are two recognized species of *Eremotherium* in North America, *E. eomigrans* from the late Blancan and early Irvingtonian of Florida (De Iuliis & Cartelle 1999) and *E. laurillardii* from the Rancholabrean (Cartelle & De Iuliis 1995). De Iuliis and Cartelle (1999) distinguished *E. eomigrans* primarily by the presence of a pentadactyl manus. All Florida Blancan and Irvingtonian *Eremotherium* are here referred to *E. eomigrans*. The panamerican *E. laurillardii* was rare in temperate North America during the Rancholabrean. The distribution of *E. laurillardii* may have become restricted to the tropics in the late Pleistocene where it is common in Central America and South America (Cartelle & De Iuliis 1995).

Florida is the only region in temperate North America where *Eremotherium* is common. Until fairly recently, *Eremotherium* was unknown from the North American Blancan record (e.g., Webb 1976), but this genus is now known to occur in six Florida late Blancan faunas (Table 1; Morgan & Hulbert 1995; De Iuliis & Cartelle 1999). Haile 7C is the type locality of *E. eomigrans*, where at least five skeletons have been recovered (De Iuliis & Cartelle 1999), including a mounted skeleton on display at the FLMNH. Early Irvingtonian records of *E. eomigrans* from Florida include Crystal River Power Plant, Haile 16A, Haile 21A, Leisey Shell

Pit, Payne Creek Mine, and Pool Branch (Morgan & Hulbert 1995; De Iuliis & Cartelle 1999). Blancan and Irvingtonian records of *Eremotherium* from Florida are far more numerous than Rancholabrean records. The only Rancholabrean fauna in Florida with a significant sample of *Eremotherium* is the Daytona Beach LF (Cartelle & De Iuliis 1995). The large sample of *E. laurillardii* from Daytona Beach includes a mounted skeleton in the Daytona Museum of Arts and Sciences.

Nothrotheriops.—There are two recognized species of *Nothrotheriops*, *N. texanus* from the Irvingtonian and *N. shastensis* from the Rancholabrean (Akersten & McDonald 1991; McDonald 1995). *N. texanus*, described based on a skull from a site in Wheeler County in the Texas Panhandle (Hay 1916), was fairly widespread in Irvingtonian faunas from Florida to the Great Plains to California and northern Mexico (Akersten & McDonald 1991; McDonald 1995). *N. shastensis* was restricted to Rancholabrean faunas in western North America, primarily the southwestern desert region (McDonald 1985, 2003). *Nothrotheriops* appears to be one of the few genera involved in the Blancan/Irvingtonian pulse of the Interchange that does not have a definite late Blancan record in North America (Akersten and McDonald 1991). Previously published late Blancan records of *Nothrotheriops* from the Temecula Arkose and the Anza-Borrego Desert, both in California, are either *Megalonyx* or are indeterminate ground sloths (Akersten & McDonald 1991; Jefferson pers. comm). The earliest undoubted records of *Nothrotheriops* are specimens referred to *N. texanus* from four early Irvingtonian sites (1.0-1.6 Ma): Leisey Shell Pit and Pool Branch in Florida (McDonald 1985, 1995); Gilliland in Texas (Hibbard & Dalquest 1966); and El Golfo in Sonora, Mexico (Shaw 1981; Shaw & McDonald 1987). Leisey Shell Pit has the largest sample of *N. texanus*, represented by numerous skulls, mandibles, and postcranial elements (McDonald 1995). At Leisey, Gilliland, and El Golfo, *N. texanus* occurs in association with *Mammuthus*, confirming an Irvingtonian age.

CHIROPTERA, PHYLLOSTOMIDAE

Desmodus.—The vampire bat *Desmodus* rarely has been recognized as a member of the Interchange fauna, although *Desmodus* probably was a participant in the primary pulse of the GABI in the late Blancan (Morgan et al. 1988; Morgan 1991). Vampire bats almost certainly evolved in South America, but they are unknown on that continent prior to the late Pleistocene

(Morgan et al. 1988; Czaplewski and Cartelle 1998). The oldest records of *Desmodus* are from late Pliocene and early Pleistocene paleokarst deposits in northern peninsular Florida (Morgan et al. 1988; Morgan 1991). Morgan (1991) hypothesized that *Desmodus* migrated northward from South America in the late Pliocene following its primary food source, the blood of large slow-moving xenarthrans such as ground sloths and glyptodonts. *Desmodus* and two other genera of vampire bats, *Diaemus* and *Diphylla*, currently are restricted to the Neotropics from Mexico southward into South America. Vampires do not presently occur in temperate North America because they are limited by cold winter temperatures north of the 10°C winter isotherm (McNab 1973), which essentially marks the northern limits of the Neotropical Region in central Mexico. A more equable climatic regime with warmer winter temperatures, possibly coupled with larger body size, permitted the vampire bat *Desmodus stockii* to inhabit the south temperate region of North America in the late Pleistocene, as far north as West Virginia and northern California (McNab 1973; Ray et al. 1988; Morgan 1991; Grady et al. 2002).

An extinct species of vampire bat, *Desmodus archaeodaptus*, is known from one late Blancan (Inglis 1A) and two early Irvingtonian (Haile 16A and Haile 21A) sites in Florida (Morgan et al. 1988; Morgan 1991). The type specimen of *D. archaeodaptus* from Haile 21A, a complete braincase, is more primitive than the braincase of the living vampire *D. rotundus*, and is considerably smaller than skulls of the large extinct late Pleistocene vampires *D. draculae* and *D. stockii* (Morgan et al. 1988; Morgan 1991). It may be significant that the earliest occurrence of *Desmodus* is from Inglis 1A (1.8-2.0 Ma) because this locality has one of the largest faunas of Interchange vertebrates of any Blancan or Irvingtonian site in North America. Inglis 1A formed during a glacial interval in the latest Pliocene when the continental shelf along the Gulf Coast would have been exposed from Florida to the Yucatan Peninsula of Mexico, providing a wide coastal savanna corridor for large mammals migrating northward from tropical America (Webb 1978). *D. archaeodaptus* survived into the early Irvingtonian in Florida (Morgan et al. 1988; Morgan 1991). *Desmodus* is unknown in the fossil record between the early Irvingtonian and the late Rancholabrean. The large extinct species, *D. stockii*, occurs in late Rancholabrean sites in Florida, West Virginia, Texas, New Mexico, Arizona, California, and the

Mexican states of Nuevo León, Mexico, and San Luis Potosí (Ray et al. 1988; Arroyo-Cabrales & Ray 1997; Grady et al. 2002). A very large extinct vampire, *D. draculae*, originally described from Venezuela (Morgan et al. 1988), has since been reported from several additional late Pleistocene sites in both South America (Czaplewski & Cartelle 1998) and North America, including Loltun Caverns in the Yucatan Peninsula of Mexico (Arroyo-Cabrales & Ray 1997) and a cave in Belize (Czaplewski et al. 2003a). The large vampires *D. stockii* and *D. draculae* went extinct in the late Pleistocene (Morgan et al. 1988; Ray et al. 1988). The smaller *D. rotundus*, which occurs from Mexico south to Argentina, is the only surviving member of the genus *Desmodus*.

CHIROPTERA, MOLOSSIDAE

Eumops.—Czaplewski (1993) identified a tooth of the large molossid bat *Eumops* cf. *E. perotis* from the Blancan McRae Wash LF in southeastern Arizona. *E. perotis* is a living species found in the southwestern United States, northern Mexico, and South America. Czaplewski (1997) also identified *Eumops* in the medial Miocene La Venta Fauna in Colombia. *Eumops* probably evolved in South America and immigrated northward into temperate North America with the remainder of the Interchange fauna. The McRae Wash LF contains no South American immigrants other than *Eumops* and is late early Blancan in age, between 2.7 and 3.0 Ma (Johnson et al., 1975), which is slightly earlier than the previously recognized first appearance of Interchange vertebrates in temperate North America at about 2.7 Ma. However, the possibility must be considered that *Eumops* flew across the Bolivar Trough prior to the formation of the Isthmus of Panama in the Pliocene. Two other species of *Eumops* occur in temperate North America, *E. floridanus* and *E. underwoodi*. *E. floridanus* was first described as the extinct species *Molossides floridanus* from the Rancholabrean Melbourne LF along the central Atlantic Coast of Florida (Allen 1932), and also occurs in two other Rancholabrean faunas in southern Florida, Monkey Jungle Hammock and Vero (Morgan 1991, 2002). This species survives as a living animal in southern peninsular Florida, and until recently was considered a subspecies of the widespread Neotropical bat *E. glaucinus* (Koopman 1971). However, a recent review of the systematics of the Florida *Eumops* established that *E. floridanus* is a valid species endemic to the Florida pen-

insula (Timm & Genoways 2004). *E. underwoodi* is a Middle American species that barely extends its range northward into Arizona, and is also known from the RanchoLabrean Lecanto 2A LF in Florida (Morgan 1991).

Tadarida.—A distal humerus of the small molossid bat *Tadarida* from the late Blancan Macasphalt Shell Pit LF in Florida (Morgan 1991; Czaplewski et al. 2003b) is the only pre-Pleistocene record of this genus from North America. An isolated lower tooth from the late Blancan Blanco LF in Texas previously referred to *Tadarida* (Dalquest 1975) has since been reidentified as a vespertilionid bat (Czaplewski et al. 2003b). The Macasphalt humerus is larger than the humerus of the extant species *Tadarida brasiliensis*, and is similar in size to that of *Tadarida constantinei* from the medial Pleistocene Slaughter Canyon Cave, New Mexico (Lawrence 1960). Other fossil samples of *Tadarida* that are larger than *T. brasiliensis*, and perhaps conspecific with *T. constantinei*, are known from two Irvingtonian cave sites, Mammoth Cave in Kentucky (Jegla & Hall 1962) and Hamilton Cave in West Virginia (Repenning & Grady 1988; Winkler & Grady 1990). *T. brasiliensis* currently inhabits the southern United States and much of Middle and South America, and is the only extant species in this genus found in temperate North America. The late Blancan record of *Tadarida* from the Macasphalt Shell Pit LF led Morgan (1991) to hypothesize that *Tadarida* may have had a South American origin in the New World, and then immigrated to North America in the late Pliocene during the Interchange. The subsequent discovery of teeth similar to *Tadarida* from the early Miocene Thomas Farm LF in Florida (Czaplewski et al. 2003b) and the absence of a pre-late Pleistocene fossil record of *Tadarida* from South America suggest another hypothesis is possible. The presence of *Tadarida*-like teeth in the early Miocene of Florida and definite fossils of *Tadarida* from the late Pliocene of Florida and the early to medial Pleistocene of Kentucky, New Mexico, and West Virginia, suggest that the New World representatives of this genus may have originated in North America. *Tadarida* may have immigrated to North America from Eurasia in the early Miocene, as this genus occurs in Oligocene and Miocene sites in Europe (Legendre 1985). The only South American fossil record of *Tadarida* is *T. brasiliensis* from a late Pleistocene cave deposit in Brazil (Czaplewski & Cartelle 1998). Thus, although *Tadarida* participated in the GABI, it appears to be a North American genus that migrated to South America during in the Interchange, not the opposite as previously suggested (Morgan 1991).

RODENTIA, ERETHIZONTIDAE

Erethizon.—Porcupines of the genus *Erethizon* were the most widespread South American immigrants during the late Blancan, with records from Florida to Arizona and southern California and north to Idaho. There have been several systematic revisions of North American fossil porcupines (White 1968, 1970; Frazier 1981). I follow the taxonomic conclusions in Frazier's (1981) review, in particular, his referral of all North American fossil porcupines to *Erethizon*. White (1968, 1970) referred North American Blancan and Irvingtonian porcupines to the tropical American genus *Coendou*. *Erethizon* is one of four Interchange mammalian genera that is first recorded in the uppermost Gauss Chron at about 2.7 Ma, with the earliest record from the Wolf Ranch LF in Arizona (Harrison 1978). Fossils of *Erethizon* are concentrated in the western United States in the late Blancan (White 1968, 1970), whereas the majority of latest Blancan and early Irvingtonian records are from Florida (Frazier 1981; Morgan & White 1995; Hulbert 1997). There are two endemic Florida Blancan species of *Erethizon*. The type and only known locality for *E. poyeri* is the latest Blancan Haile 7C LF (Hulbert 1997). The type locality of *E. kleini* is the latest Blancan Inglis 1A LF, although this species also was reported from a site of probable early Irvingtonian age on Merritt Island on the Atlantic Coast of Florida (Frazier 1981). All other *Erethizon* records from Florida Irvingtonian sites have been referred to the living species *E. dorsatum*, including Haile 16A and Leisey Shell Pit (Table 2; Martin 1974; Frazier 1981; Morgan & White 1995). The oldest record of *E. dorsatum* is the earliest Irvingtonian Haile 16A LF. *E. dorsatum* occurs in several late Pleistocene sites in Florida (Morgan & White 1995), although this species is now absent from Florida and elsewhere on the Atlantic and Gulf coastal plains. The living porcupine is a common inhabitant of coniferous forests in the north temperate region of North America, and also occurs in the desert southwest and northern Mexico.

RODENTIA, HYDROCHAERIDAE

Hydrochaeris.—The only species of the living capybara genus *Hydrochaeris* known from temperate North America is the extinct species *Hydrochaeris holmesi*, originally described from the RanchoLabrean Sabertooth Cave in northern Florida (Simpson 1928). The spelling of *Hydrochaeris* used here follows the recommendation of Husson (1978), although the spelling *Hydrochoerus* is more common in the literature (e.g.,

Simpson 1928; Kurtén & Anderson 1980; Ahearn 1981). Mones (1984) regarded all fossil *Hydrochaeris* in North America as misidentifications of *Nechoeris*, and he called this species *N. holmesi*. The species *holmesi* is here retained in *Hydrochaeris* pending a revision of North American capybaras. *H. holmesi* occurred from the late Blancan through the Rancholabrean. This species was restricted to the southeastern United States, with the possible exception of a late Pleistocene record from Honduras (Ahearn 1981; Webb & Perrigo 1984). The earliest North American records of *H. holmesi* are from Haile 15A and Santa Fe River 4A (Ahearn 1981). *Hydrochaeris* occurs in association with *Nannippus* at both of these sites. The Inglis 1A LF has a large sample of *H. holmesi* (Ahearn 1981). The only Irvingtonian record of *H. holmesi* is Coleman 2A LF (Martin 1974; Ahearn 1981). There are Rancholabrean records of *H. holmesi* throughout the Florida peninsula, as well as the Savannah River in Georgia, Ashley River and Darlington in South Carolina, and the Orillas del Humuya Fauna in Honduras (Kurtén & Anderson 1980; Ahearn 1981; Webb & Perrigo 1984). *H. holmesi* went extinct at the end of the Rancholabrean. The living capybara *H. hydrochaeris* just barely extends its range into tropical North America in southern Panama (Eisenberg 1989).

Nechoeris.—The large extinct capybara genus *Nechoeris* had a limited, disjunct distribution in temperate North America during the late Blancan where it is known from two sites in Arizona and five sites in Florida (Ahearn & Lance 1980; Morgan & White 1995). *Nechoeris* is restricted to the southeastern United States in the Irvingtonian and Rancholabrean, although other species of the genus are known from Pleistocene sites in Middle and South America. The widespread occurrence of *Nechoeris* in tropical North America (Miller & Carranza-Castañeda 1984; Webb & Perrigo 1984; Carranza-Castañeda & Miller 1988) and in South America (Mones 1984) is similar to the Plio-Pleistocene distribution of *Eremotherium*. Ahearn (1981) reviewed the North American fossil hydrochaerids. Ahearn and Lance (1980) described the species *Nechoeris dichroplax* from the late Blancan Dry Mountain (=111 Ranch) fauna in southeastern Arizona (Galusha et al. 1984), with referred material from two late Blancan sites in southern Florida, Sommer's Pit and Mule Pen Quarry. Morgan and White (1995) referred specimens to *N. dichroplax* from the Macasphalt Shell Pit and Kissimmee River LFs in southern Florida. An isolated tooth of *Nechoeris* from the latest Blancan Haile 7C LF in Florida can not be identified to species (Hulbert

1997). Early Irvingtonian fossils of *Nechoeris* from the Leisey Shell Pit and Apollo Beach LFs in Florida differ from both *N. dichroplax* and *N. pinckneyi* from the Rancholabrean, and may represent an undescribed species. The Leisey *Nechoeris* sample lacks the diagnostic M3; however, M3s of *Nechoeris* from the correlative Apollo Beach LF, located along the Gulf Coast just north of Leisey (Table 2), differ from *N. dichroplax* in lacking bifurcated plates and are smaller than *N. pinckneyi*. The very large species *N. pinckneyi* is restricted to Rancholabrean faunas and is well known from Florida (Kurtén & Anderson 1980; Ahearn 1981). There are also records of *N. pinckneyi* from the Atlantic Coastal Plain in North Carolina and South Carolina and the Gulf Coastal Plain in Louisiana and Texas (Kurtén & Anderson 1980; Phillips et al. 2001).

Nechoeris is one of four genera of South American immigrant mammals that first appeared in the southwestern United States at about 2.7 Ma. Galusha et al. (1984) recorded *N. dichroplax* from the uppermost Gauss Chron just below the Gauss/Matuyama boundary from 111 Ranch in the Safford Basin of southeastern Arizona. Latest Blancan and early Irvingtonian records of *Nechoeris* are restricted to Florida, and most consist of fossils that cannot be identified to the species level. The Florida early Irvingtonian samples suggest there is an undescribed Irvingtonian species of *Nechoeris* from Florida.

DISCUSSION

EVOLUTION AND BIOGEOGRAPHY OF THE INTERCHANGE FAUNA IN FLORIDA

The Great American Biotic Interchange in temperate North America began in the late Miocene at about 9 Ma. From that time onward, until the extinction of the Pleistocene megafauna at about 11 ka, most well-sampled vertebrate faunas from Florida contain one or more species of mammals that either emigrated from South America or evolved from a species of Neotropical origin. Each of the Interchange genera of mammals and birds has a distinct evolutionary and biogeographic history in temperate North America discussed in detail above. The following is a summary of the larger evolutionary and biogeographic trends of the Florida Interchange fauna. Taking into account recent synonymies and descriptions of new species, there are 21 genera and 42 species of mammals and birds of South American ancestry recorded from Late Neogene faunas in temperate North America. Among the 21 genera of South American origin found in North America, all but

one genus, the giant anteater *Myrmecophaga*, are known from Florida. The 20 Interchange genera known from Florida include 11 genera endemic to North America (*Titanis*, *Teratornis*, *Aiolornis*, *Pachyarmatherium*, *Glyptotherium*, *Thinobadistes*, *Paramylodon*, *Pliometanastes*, *Megalonyx*, *Nothrotheriops*, and *Erethizon*) and nine genera that occur in both North America and South America (*Didelphis*, *Dasyopus*, *Holmesina*, *Glossotherium*, *Eremotherium*, *Desmodus*, *Eumops*, *Hydrochaeris*, and *Nechoerus*). Among the 42 species of Interchange vertebrates, 33 species occur in Florida (Tables 1-2), of which 31 species are endemic to North America and only two species occur in both North and South America, *Glossotherium chapadmalense* and *Eremotherium laurillardi*.

The South American immigrants that reached temperate North America during the primary pulse of the Interchange in the late Blancan and early Irvingtonian consist of 18 genera (excluding *Megalonyx*, *Pliometanastes*, and *Thinobadistes*), and can be divided into three groups on the basis of their distribution in North American Blancan and Irvingtonian faunas. Eight genera are known primarily or exclusively from Florida: *Titanis*, *Teratornis*, *Dasyopus*, *Holmesina*, *Pachyarmatherium*, *Eremotherium*, *Desmodus*, and *Hydrochaeris*. Eight genera are more widespread, particularly across the southernmost tier of states (Florida, Texas, New Mexico, Arizona, and California): *Aiolornis*, *Didelphis*, *Glyptotherium*, *Nothrotheriops*, *Glossotherium*, *Paramylodon*, *Erethizon*, and *Nechoerus*. Two genera are each known from a single pre-Rancholabrean site in North America, *Myrmecophaga* from the early Irvingtonian El Golfo LF in northwestern Mexico and *Eumops* from the late early Blancan McRae Wash LF in Arizona (Shaw & McDonald 1987; Czaplewski 1993). *Myrmecophaga* and *Eumops* are the only two Interchange genera that are unknown from Florida Blancan and Irvingtonian sites, although *E. floridanus* is an endemic species that still inhabits southern Florida and is also known from several late Pleistocene cave deposits in the southern part of the state (Morgan 2002; Timm and Genoways 2004) and *E. underwoodi* occurs in a single Rancholabrean site in Florida (Morgan 1991). Among the eight widely-distributed genera, the largest Interchange samples of *Nothrotheriops*, *Glossotherium*, *Paramylodon*, and *Erethizon*, are from Florida. Only *Aiolornis*, *Glyptotherium*, and *Nechoerus* are better known from Blancan and/or Irvingtonian fossil sites outside of Florida. Most records of *A. incredibilis* are from Blancan and

early Irvingtonian sites in southern California, with a record from the early Irvingtonian Leisey Shell Pit in Florida (Emslie 1995a; Campbell et al. 1999). The most complete material of the glyptodonts *G. texanum* and *G. arizonae* (Gillette & Ray 1981) is from late Blancan sites in Arizona, Texas, and New Mexico. The largest sample of the late Blancan capybara *N. dichroplax* is from 111 Ranch in Arizona (Ahearn & Lance 1980). Irvingtonian records of *Nechoerus* are restricted to Florida.

After the primary pulse of the Interchange ceased in the early Irvingtonian (about 1.5 Ma), most of the South American immigrants became integral members of the temperate North American fauna, and underwent a long period of autochthonous evolution during the remainder of the Irvingtonian and Rancholabrean unrelated to their Neotropical origin. The only South American mammals that reached temperate North America after the early Irvingtonian, exclusive of bats, were *Didelphis* in the medial Irvingtonian and *Dasyopus novemcinctus* in the Holocene. Among the Interchange genera from the late Blancan or early Irvingtonian in Florida, two genera went extinct shortly after their arrival leaving no apparent descendants (*Glossotherium* [but see below], *Pachyarmatherium*), nine genera seemingly disappeared in the medial to late Irvingtonian and then reappeared in the Rancholabrean (*Titanis*, *Aiolornis*, *Teratornis*, *Glyptotherium*, *Eremotherium*, *Desmodus*, *Nechoerus*, and *Hydrochaeris*), and the remainder of the genera inhabited North America throughout the Irvingtonian and Rancholabrean, two of which still survive (*Dasyopus*, *Holmesina*, *Megalonyx*, *Paramylodon*, *Nothrotheriops*, and *Erethizon*).

Glossotherium and *Pachyarmatherium* arrived during the primary pulse of the Interchange in the late Blancan/early Irvingtonian, but are unknown after that time. *Glossotherium* is known only from early late Blancan faunas in North America, whereas the endemic North American mylodont *Paramylodon* occurs in latest Blancan and younger faunas. However, the absence of *Glossotherium* from faunas younger than about 2.2 Ma may be a taxonomic artifact. It appears likely that Blancan *Glossotherium* should be placed in *Paramylodon*, and that specimens from Florida and elsewhere referred in the South American Pliocene species *G. chapadmalense* probably belong to an endemic North American species, possibly *Glossotherium* (= *Paramylodon*?) *garbanii*. If these taxonomic assignments are correct, then *Paramylodon* was a wide-ranging genus that occurred from the late Blancan

through the end of the Rancholabrean. *Pachyarmatherium leiseyi* was restricted to the southeastern United States in the late Blancan and early Irvingtonian, and is unknown after the late early Irvingtonian (about 1.0 Ma).

Titanis, *Aiolornis*, *Teratornis*, *Glyptotherium*, *Eremotherium*, *Desmodus*, *Nechoerus*, and *Hydrochaeris*, arrived in temperate North America during the Blancan or early Irvingtonian, are mostly absent from the fossil record during the medial and late Irvingtonian (~0.3-1.0 Ma), and then reappeared in the Rancholabrean, or Recent in the case of one genus. Presumably, these ten genera survived in tropical Middle America during much of the Irvingtonian, and then reinvaded temperate North America in the Rancholabrean. Corroboration of this hypothesis depends upon an Irvingtonian fossil record from Middle America, which at present is virtually non-existent. This pattern could also be an artifact of the fossil record since most of these genera are rare. Furthermore, medial to late Irvingtonian and early Rancholabrean faunas are not particularly common in the southern states where these taxa most likely would have occurred. *Titanis walleri* was thought to have gone extinct shortly after it arrived in the late Blancan, with the youngest record of this species in Florida from the latest Blancan Inglis 1A LF (Webb 1976; Emslie 1998). However, a record of *Titanis* from a Rancholabrean site on the Texas Gulf Coastal Plain (Baskin 1995) suggests this giant flightless bird may have survived in Middle America during much of the Pleistocene. Emslie (1995a) described a sample of *Teratornis merriami* from the early Irvingtonian Leisey Shell Pit., whereas most other records of *Teratornis* are from the Rancholabrean (Brodkorb 1964). The small extinct vampire bat *Desmodus archaeadaptus* is known from one latest Blancan site and two early Irvingtonian sites in Florida. The next oldest records of vampire bats are of the larger extinct species *D. stockii* from late Rancholabrean cave deposits in Florida, West Virginia, Texas, New Mexico, Arizona, California, and Mexico (Morgan et al. 1988; Ray et al. 1988; Arroyo Cabrales & Ray 1997; Grady et al 2002).

The earliest glyptodont in Florida is *G. arizonae* from several early late Blancan (2.2-2.7 Ma) sites (Table 1). Sites of similar age in Texas (Mt Blanco and Cita Canyon) and Arizona (111 Ranch) have the smaller species *G. texanum*. *G. arizonae* also occurs in several latest Blancan (1.8-2.2 Ma) sites in Florida (Table 1), as well as latest Blancan (Curtis Ranch, Virden) and early

Irvingtonian (Gilliland, Holloman) sites in the southwestern United States. Leisey Shell Pit is the only early Irvingtonian record of *Glyptotherium* from Florida. There are no glyptodonts in Florida or elsewhere in temperate North America between the end of the early Irvingtonian (about 1.0 Ma) and the beginning of the Rancholabrean (about 0.3 Ma). *Glyptotherium* reappeared in the southeastern United States in the Rancholabrean, represented by the small species *G. floridanum*, and survived there until it went extinct at the end of the Rancholabrean. There are numerous records of *G. floridanum* from peninsular Florida and the Gulf Coastal Plain of Texas, with an outlying record from South Carolina (Gillette & Ray 1981). *Eremotherium* is restricted to Florida during the Blancan and Irvingtonian. *E. eomigrans* occurs in Florida faunas ranging in age from early late Blancan through the early Irvingtonian. *Eremotherium* is unknown from Florida and elsewhere in temperate North America during the medial and late Irvingtonian (Morgan & Hulbert 1995). The widely-distributed species *E. laurillardii* occurred in North, Middle, and South America during the late Pleistocene. This species is rare in Florida Rancholabrean faunas, except for the Daytona Beach LF (Cartelle & De Iuliis, 1995). *E. laurillardii* also occurs in Rancholabrean sites in South Carolina, Georgia, Texas, and throughout Central America (Gazin 1957; Kurtén & Anderson 1980; Webb & Perrigo 1985; Lucas et al., 1997). The capybara genera *Nechoerus* and *Hydrochaeris* are primarily restricted to Florida during the Blancan and Irvingtonian, except for two late Blancan records of *Nechoerus* from Arizona (Ahearn & Lance 1980; Ahearn 1981). All other Interchange records of *Nechoerus* are from Florida, including *N. dichroplax* from four late Blancan faunas and an apparently undescribed species from two early Irvingtonian faunas (Ahearn & Lance 1980; Ahearn 1981; Morgan & Hulbert 1995). *Nechoerus* is unknown from medial and late Irvingtonian sites in temperate North America. The giant capybara *N. pinckneyi* reappears in the Rancholabrean where it is known from Florida and the southeastern United States (Kurtén & Anderson 1980). *Hydrochaeris* occurs in three late Blancan sites in Florida (Ahearn 1981), and then does not reappear until the latest Irvingtonian Coleman 2A LF (Martin 1974). *H. holmesi* is fairly common in Florida Rancholabrean faunas but is unknown elsewhere in temperate North America (Kurtén & Anderson 1980; Ahearn 1981). Webb and Perrigo (1985) tentatively identified *H. holmesi* from a late Pleistocene site in Honduras.

The remainder of the Interchange fauna, including *Dasypus*, *Holmesina Megalonyx*, *Paramylodon*, *Nothrotheriops*, and *Erethizon*, consists of genera that inhabited temperate North America throughout the Irvingtonian and Rancholabrean. *Megalonyx*, *Paramylodon*, and *Erethizon* became very widespread, occurring essentially throughout temperate North America (Kurtén & Anderson 1980; McDonald 2003). *Megalonyx* had become widely distributed by the late Hemphillian (*M. curvidens* and *M. mathisi*), and certainly during the Blancan (*M. leptostomus*), with records from the Great Plains (Oklahoma, Kansas, and Nebraska) and the Pacific Northwest (Oregon, Washington, and Idaho), as well as Florida, Texas, and California. *Megalonyx* continued to occur widely during the Irvingtonian (*M. wheatleyi*) and Rancholabrean (*M. jeffersonii*). *M. jeffersonii* was the most widespread member of the South American fauna during the Rancholabrean, with records from the Atlantic to the Pacific, as far north as Alaska and the Yukon and Northwest Territories of Canada, and as far south as southern Mexico, although it was uncommon in the western deserts and mountains (McDonald 1977, 2003, this volume). *Paramylodon harlani* survived for about 2 Ma, from the latest Blancan through the late Rancholabrean, and was found from the Atlantic to the Pacific and as far north as Washington and Montana and south to southern Mexico (Kurtén & Anderson 1980; McDonald 1995, 2003, this volume). Several extinct species of *Erethizon* occurred in the late Blancan from Florida to southern California and north to Idaho, and the living porcupine *E. dorsatum* first appeared in the early Irvingtonian (Frazier 1981). From its earliest appearance in the late Blancan until the present, *Erethizon* appears to have inhabited temperate forests. *Erethizon* is absent from tropical North America where it is replaced by the prehensile-tailed porcupine *Coendou*, an inhabitant of tropical rain forests in Middle America and South America (Eisenberg 1989). *Coendou* (*sensu* Frazier 1981) lacks a North American fossil record.

The small megatheriid ground sloth *Nothrotheriops* first appears in the early Irvingtonian. *N. texanus* was fairly widespread in southern North America during the Irvingtonian, from Florida to Texas to California and northwestern Mexico (Akersten & McDonald 1991; McDonald 1995). After the Irvingtonian, *Nothrotheriops* apparently became restricted to western North America (McDonald 1985, 1995). The Rancholabrean species *N. shastensis* is most common in cave deposits in the desert southwest from south-

western Texas to California, and also occurs as far south as central Mexico (McDonald 1985; Akersten & McDonald 1991; McDonald 2003).

Both *Dasypus* and *Holmesina* have fairly continuous fossil records in Florida from the late Blancan through the late Rancholabrean. Only during the late Rancholabrean do these two genera regularly occur outside of Florida. *D. bellus* underwent a significant size increase from its first appearance in the late Blancan until its extinction at the end of the Rancholabrean (Robertson 1976). The earliest non-Florida record of *D. bellus* is from the late Blancan Big Springs LF in Nebraska (Voorhies, 1987). *D. bellus* became fairly widespread in the late Rancholabrean, with records from as far north as Iowa, Missouri, Illinois, and Indiana, and as far west as Texas and New Mexico (Kurtén & Anderson 1980). *H. floridanus* is restricted to the late Blancan and early Irvingtonian of Florida, except for the early Irvingtonian Gilliland LF in Texas (Hibbard & Dalquest 1966; Hulbert & Morgan 1993). The larger *H. septentrionalis* occurs from the medial Irvingtonian through the late Rancholabrean in Florida (Hulbert & Morgan 1993), as well as Rancholabrean sites in Texas, Oklahoma, and Kansas (Kurtén & Anderson 1980; Edmund 1985a).

The fossil record of Interchange bats is poor, particularly prior to the late Pleistocene. The vampire bat *Desmodus* has the best fossil record of any Interchange bat. Several other species of phyllostomids and molossids are discussed here. The presumed Interchange bat fauna includes only three genera from Florida: *Desmodus* in the late Blancan and early Irvingtonian, *Eumops* in the Rancholabrean, and *Tadarida* in the late Blancan and Rancholabrean. Three genera of phyllostomid bats, a family of South American origin (Koopman 1982), occur in the modern fauna of temperate North America, *Choeronycteris*, *Leptonycteris* and *Macrotus*. *Macrotus waterhousii* occurs in a Pleistocene deposit in the Little Thirty-eight cinnabar mine near Terlingua in the Big Bend region of Texas (Ray & Wilson 1979). *Leptonycteris nivalis* is known from the Rancholabrean San Josecito Cave in the state of Nuevo León, northern Mexico (Jones 1958). *Choeronycteris mexicana* and *Leptonycteris curasoae* have no fossil record. The earliest North American record of *Eumops* is from the late early Blancan (~3.0 Ma) of Arizona. *Eumops* does not reappear in North America until the late Pleistocene, with Rancholabrean records of *E. floridanus* and *E. underwoodi* from Florida (Morgan 1991, 2002). All three species of *Eumops* with a fossil record in temper-

ate North America occur in the modern fauna in the southernmost United States. A distal humerus of *Tadarida* from the Macasphalt Shell Pit is the earliest temperate North American record of this genus. The Macasphalt *Tadarida* is larger than the living species *T. brasiliensis*, and is similar in size to the extinct species *T. constantinei* from the medial Pleistocene of New Mexico. Irvingtonian specimens of *Tadarida* from Mammoth Cave, Kentucky and Hamilton Cave, West Virginia are also larger than *T. brasiliensis* and are similar to *T. constantinei*. *T. brasiliensis* is known from late Rancholabrean faunas in Florida, New Mexico, and Arizona (Kurtén & Anderson 1980; Morgan 1991; Harris 1993).

The only other bats with Neotropical affinities that have a Late Neogene fossil record in temperate North America are two species in the family Mormoopidae, *Pteronotus pristinus* and *Mormoops megalophylla*. The Mormoopidae was long thought to have a South American origin based on the modern Neotropical distribution of this family; however, recent discoveries of Oligocene mormoopids from Florida indicate this family probably originated in North America (Morgan & Czaplewski 2002). Mormoopids apparently disappeared from temperate North America in the Oligocene and survived in tropical Middle America throughout the Neogene. The next youngest fossil record of the Mormoopidae is a partial skeleton referred to the extant species *Pteronotus parnellii* from the Irvingtonian (?) Barranca del Sisimico site in El Salvador (Webb & Perrigo 1984). *Pteronotus pristinus* and *Mormoops megalophylla* are known from late Pleistocene sites in Florida (Morgan 1991, 2002). *P. pristinus* is an extinct species known elsewhere only from Cuba, whereas *M. megalophylla* is an extant species found in the southwestern United States, Middle America, and northern South America.

GEOCHRONOLOGY OF THE INTERCHANGE FAUNA IN FLORIDA

The appearance of South American vertebrates during the Late Neogene defines the onset of the Great American Biotic Interchange in Florida and elsewhere in temperate North America. The immigration of these Neotropical taxa occurred primarily during two restricted time intervals: early Hemphillian (late Miocene, 7-9 Ma) and late Blancan/early Irvingtonian (late Pliocene and early Pleistocene, 1.0-2.7 Ma). The remainder of the late Miocene, Pliocene, and Pleistocene, from the late Hemphillian through the early Blancan (2.7-7.0 Ma) and the medial Irvingtonian through the end of the

Rancholabrean (10 ka-1.0 Ma), was characterized by the autochthonous evolution of the South American taxa that arrived during the two short-lived immigration events. The general time ranges for the first appearances of the 20 South American Interchange genera found in Florida are as follows: two genera (*Pliometanastes* and *Thinobadistes*) immigrated in the early Hemphillian (8-9 Ma); one genus (*Megalonyx*) appeared in the late Hemphillian (~7 Ma) apparently having evolved in North America from *Pliometanastes*; 12 genera (*Titanis*, *Dasyops*, *Pachyarmatherium*, *Holmesina*, *Glyptotherium*, *Glossotherium*, *Paramylodon*, *Eremotherium*, *Desmodus*, *Erethizon*, *Hydrochaeris*, and *Neochocerus*) first appeared in the late Blancan (1.8-2.7 Ma); two genera (*Teratornis* and *Nothrotheriops*) are first recorded in the early Irvingtonian (1.0-1.8 Ma); and one genus (*Didelphis*) did not arrive until the medial Irvingtonian (0.8-1.0 Ma). With several exceptions noted below, the earliest appearance of these 20 Interchange genera in Florida closely approximates their earliest appearance elsewhere in temperate North America.

The first South American mammals to participate in the Great American Biotic Interchange, the ground sloths *Pliometanastes* and *Thinobadistes*, both have their first appearance datum (FAD) in North America at the beginning of the Hemphillian at about 9 Ma. The youngest record of *Thinobadistes* is from the early late Hemphillian (Hh3, about 7 Ma) Coffee Ranch LF of Texas (Webb 1989). *Thinobadistes* went extinct in the late Hemphillian and left no descendants. The earliest records of *Pliometanastes protistus* from the earliest Hemphillian of Florida (8.5-9.0 Ma), although the oldest absolute date for the genus is from the Siphon Canal LF in California with an underlying K/Ar date of 8.19 Ma (Hirschfeld & Webb 1968; Hirschfeld 1981). *Megalonyx* is an endemic North American genus that apparently evolved from *Pliometanastes* in the late Hemphillian (Webb & Perrigo 1984). The only Hemphillian record of *Megalonyx* from Florida is from the latest Hemphillian (Hh4, ~5 Ma) Palmetto Fauna from the Bone Valley Formation. There are several somewhat older records of *Megalonyx* in early late Hemphillian (Hh3, ~6-7 Ma) faunas in Nebraska and Oklahoma.

The early Blancan (2.7-4.9 Ma) was a depauperate time period for the Interchange fauna in temperate North America, represented by a single autochthonous (non-immigrant) species, *Megalonyx leptostomus*. All known Florida early Blancan faunas are marine and lack Interchange mammals (Morgan 1994). However, four genera of South American Interchange mammals,

Glyptotherium, *Plaina*, *Glossotherium*, and *Nechoerus*, are recorded from early Blancan deposits in central Mexico (Carranza-Castañeda & Miller 2004; Flynn et al 2005). The primary pulse of the GABI in temperate North America, comprising 15 genera of South American immigrants, occurred during the late Blancan and early Irvingtonian, beginning about 2.7 Ma and continuing until about 1.5 myr. Within this period of slightly longer than 1 Ma, the FAD of 10 of these 15 genera occurred during the early late Blancan (2.2-2.7 Ma). The FAD for the individual taxa has been determined by their occurrence in faunas with associated radioisotopic dates and/or paleomagnetic stratigraphy, primarily in southwestern late Blancan sites or, for most Florida sites, by biochronologic comparisons. The biostratigraphic correlations for the early late Blancan depend primarily on the co-occurrence of the South American immigrant taxa with one or more genera of autochthonous North American mammals (e.g., *Borophagus*, *Hypolagus*, *Nannippus*, *Rhynchotherium*) that disappeared at about 2.2 Ma (*Nannippus* extinction datum of Lindsay et al. 1984). The first undoubted Blancan immigrants in temperate North America appeared in sites dating to the uppermost Gauss Chron, just prior to the Gauss/Matuyama boundary at 2.58 Ma. By convention, these immigrants in the uppermost Gauss Chron are usually assigned a FAD of 2.7 Ma, which also defines the beginning of the late Blancan (Woodburne & Swisher 1995). Four genera of immigrants have their FAD at 2.7 Ma, *Glyptotherium*, *Glossotherium*, *Erethizon*, and *Nechoerus*. The earliest precisely dated temperate North American records for these genera are from the following sites, all of which have associated paleomagnetic data placing them in the uppermost Gauss Chron: *Glyptotherium* (111 Ranch, Arizona; Mesilla A, New Mexico; Cita Canyon and Hudspeth, Texas), *Glossotherium* (Pearson Mesa, New Mexico; Cita Canyon; Donnelly Ranch, Colorado), *Erethizon* (Wolf Ranch, Arizona), and *Nechoerus* (111 Ranch).

No Florida late Blancan sites are definitively dated to the upper Gauss Chron, although *Glyptotherium*, *Glossotherium*, and *Nechoerus*, are recorded from Florida early late Blancan sites (2.2-2.7 Ma) in association with *Nannippus*, and are thus similar in age to the FAD of these three genera from sites in the southwestern United States (Table 1). *Glyptotherium* occurs in four early late Blancan sites in Florida, Brighton Canal, Kissimmee River, Santa Fe River 1, and St. Petersburg Times. *Glossotherium* has been identified from five early late Blancan sites in Florida, Haile 15A, Lehigh

Acres, Kissimmee River, Macasphalt Shell Pit, and Santa Fe River 1. *Nechoerus* is known from four Florida early late Blancan sites, Kissimmee River, Macasphalt Shell Pit, Mule Pen Quarry, and Sommer's Pit. Six other genera of South American immigrants that are primarily restricted to Florida have their FAD in the early late Blancan: *Titanis*, *Dasyus*, *Pachyarmatherium*, *Holmesina*, *Eremotherium*, and *Hydrochaeris*. Macasphalt Shell Pit records the association of *Dasyus* and *Holmesina* with *Nannippus* and *Rhynchotherium*, and has associated magnetostratigraphy indicating correlation with the lower Matuyama Chron (2.15-2.58 Ma). *Titanis*, *Pachyarmatherium*, *Eremotherium*, and *Hydrochaeris* are not known from Macasphalt, but occur in other Florida sites in association with *Nannippus*, indicating an early late Blancan age. Florida sites documenting the early late Blancan FAD of these genera are *Titanis* (Santa Fe River 1), *Pachyarmatherium* (El Jobean, Kissimmee River), *Eremotherium* (Brighton Canal, Kissimmee River, Lehigh Acres); and *Hydrochaeris* (Haile 15A).

Paramylodon and *Desmodus* have their FAD in the latest Blancan. The first appearance of *Paramylodon* may not represent a separate immigration event, as it is likely that *Paramylodon* is either congeneric with, or evolved from, *Glossotherium*. Bats are so rare in Blancan sites that the first appearance of *Desmodus* must be considered a minimum age, pending the discovery of additional late Blancan sites of karst origin in Florida. The earliest occurrence of both *Paramylodon* and *Desmodus* is the latest Blancan (1.8-2.0 Ma) Inglis 1A LF from Florida.

Teratornis and *Nothrotheriops* have their FAD in the early Irvingtonian, between 1.5 and 1.8 Ma. The earliest record of *Teratornis* is from the early Irvingtonian Leisey Shell Pit in Florida at about 1.5 Ma (Emslie 1995a). Late Blancan and early Irvingtonian teratorns previously referred to *Teratornis incredibilis* recently were transferred to *Aiolornis* (Campbell, et al. 1999). The earliest records of *Nothrotheriops* are from several broadly correlative early Irvingtonian sites, including Leisey Shell Pit and Pool Branch in Florida, Gilliland in Texas, Anza-Borrego Desert in southern California, and El Golfo in northwestern Mexico (Hibbard & Dalquest 1966; Shaw & McDonald 1987; McDonald 1995; Morgan & Hulbert 1995). The absence of *Nothrotheriops* from late Blancan sites and its presence in at least five widely distributed early Irvingtonian faunas indicates that this genus might be useful in defining the beginning of the Irvingtonian. With the excep-

tion of *Didelphis*, no other first appearances of Interchange genera are known from temperate North American sites younger than Leisey, suggesting that the primary pulse of the GABI had already ceased by about 1.5 Ma. The FAD of the opossum *Didelphis* is medial Irvingtonian (0.8-1.0 Ma), with the earliest record from Fyllan Cave in Texas (Winkler & Gose 2003). The next oldest records are the late Irvingtonian Coleman 2 and Sebastian Canal sites in Florida (Martin 1974; Morgan & Portell 1996).

FINAL COMMENTS

Recent discoveries in central Mexico (Carranza-Castañeda & Miller 2004; Flynn et al. 2005) and the Amazonian region of Peru (Campbell et al. 2000, 2001) suggest that the primary pulse of the Great American Biotic Interchange in tropical latitudes may have begun as early as the late Miocene (dates from Peru) or early Pliocene (dates from central Mexico). These new data differ significantly from the prevailing theory that the early "heralds" of the Interchange reached temperate latitudes in North America (*Pliometanastes* and *Thinobadistes*) and South America (*Cyonasua*) in the late Miocene (~7-9 Ma) by overwater dispersal or island hopping across the Bolivar Trough (e.g., Webb 1976, 1978, 1985, 1991), and that the primary pulse of the GABI did not begin until the formation of the Panamanian Isthmus in the late Pliocene (~3 Ma).

It is possible that some Florida Blancan sites lacking external geochronologic control (Haile 15A, Kissimmee River, Santa Fe River 1) may actually be older than 2.7 Ma. Among Florida late Blancan sites, only the Macasphalt Shell Pit has associated geochronologic data (paleomagnetic stratigraphy) that constrain its age to between 2.2 and 2.6 Ma. The other Florida sites of supposed late Blancan age have been dated by biochronology based on their faunal similarity to Macasphalt Shell Pit and to southwestern late Blancan Interchange sites that date to the early late Blancan (2.2-2.7 Ma). Perhaps corridors for dispersal from Middle America to Florida opened earlier in the Blancan along the Gulf of Mexico coastal plain (Gulf Coast savanna corridor of Webb 1978), since Florida was probably the only region in temperate North America that had a subtropical climate in the Pliocene. However the pre-Interchange portion of the Pliocene (~2.7-4.9 Ma) apparently was a period of high sea level, about 50 m above present (Dowsett & Cronin 1990), which would have led to the submergence of the low-elevation terrain on the Gulf Coastal Plain, as well as much of the Florida peninsula. It may be significant that marine vertebrates

occur in two Florida Blancan Interchange faunas deposited from 10 m (Kissimmee River) to 30 m (Haile 15A) above present sea level.

Only more precise dating will shed additional light on the age of Florida Blancan Interchange vertebrate faunas. Unfortunately, the Florida Neogene stratigraphic sequence lacks volcanic rocks that can be radioisotopically dated and most sediments in the state are not suitable for paleomagnetic analysis, although two Florida sites (Macasphalt Shell Pit and Leisey Shell Pit) have yielded promising results from magnetostratigraphy (MacFadden 1995; Jones et al. 1991). Techniques such as uranium-lead dating (Getty et al. 2001), strontium isotope chronostratigraphy (Jones et al. 1991, 1995), and refined sea level data may in the future provide more precise geochronologic control for Florida Late Neogene vertebrate faunas (Morgan 1993).

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