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Tropical and western influences in vertebrate faunas from the Pliocene and Pleistocene of Florida

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ABSTRACT

Extralimital and extinct species of birds and mammals with either tropical or western affinities are characteristic of numerous Florida Pliocene and Pleistocene vertebrate faunas. These sites document nonanalog or disharmonious faunas, recording the association of certain genera or species that are no longer sympatric, in particular taxa now restricted to drier habitats in western North America or tropical habitats in Middle America occurring together with species still found in Florida and the southeastern United States. Extralimital or extinct taxa of western origin in Florida Plio-Pleistocene nonanalog faunas include: the mammals *Antrozous*, *Lepus*, *Spermophilus*, *Thomomys*, and *Baiomys*; and the birds *Gymnogyps californianus*, *Teratornis merriami*, *Aquila chrysaetos*, *Tympanuchus cupido*, two species of *Glaucidium*, and *Pica pica*. A large influx of tropical species occurred in Florida late Blancan and early Irvingtonian sites, primarily consisting of taxa of South American origin involved in the Great American Biotic Interchange. Besides large Interchange mammals, other mammals with tropical affinities now extinct or extralimital to Florida include: the bats *Desmodus archaeodaptes*, *Desmodus stocki*, *Mormoops megalophylla, Pteronotus pristinus*, and *Eumops underwoodi*, the carnivores *Leopardus pardalis*, *Leopardus wiedii*, *Panthera onca*, two species of *Conepatus*, and *Tremarctos floridanus*, and the peccary *Pecari*. Tropical birds in Florida Plio-Pleistocene faunas include the extralimital *Tachybaptus dominicus*, *Laterallus exilis*, *Jacana spinosa*, *Buteogallus urubitinga*, *Milvago chimachima*, *Vanellus chilensis*, and *Ceryle torquata*; as well as several extinct species including *Titanis walleri*, a chachalaca (Family Cracidae), *Amplibuteo concordatus*, *Spizaetus grinnelli*, and *Cremaster tytthus*. These tropical and western taxa indicate the presence of biogeographic corridors during Plio-Pleistocene glacial intervals that connected the Florida peninsula to both the arid western United States and tropical Middle America. A mosaic of desert grassland and savanna habitats intermixed with wetlands apparently extended eastward from the arid Southwest through Texas and along a southeastern corridor to the Florida peninsula. A Gulf Coast savanna corridor supporting savanna and thorn scrub habitats probably existed during glacial low sea level stands on the exposed continental shelf and coastal plain along the northern margin of the Gulf of Mexico, connecting the Florida peninsula with Mexico and Central America. The occurrence of both tropical and western taxa in some of the same faunas strongly indicates that these distributional patterns were contemporaneous and corresponded to climatic conditions and vegetational associations that no longer exist in Florida.

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1. Introduction

Florida has the most complete record of late Pliocene and Pleistocene terrestrial vertebrates in eastern North America (Hulbert, 2001). Florida mammalian faunas from the late Pliocene through the medial Pleistocene (Blancan and Irvingtonian land mammal ages) have been reviewed (Morgan and Hulbert, 1995), as have many of the important Plio-Pleistocene avifaunas (Emslie, 1992, 1995, 1998). However, Florida sites have not been studied in the context of nonanalog or disharmonious faunas; species found together in fossil faunas that do not co-occur at the present time. Although originally called “disharmonious” faunas, it appears that these faunas were “in harmony” with the climatic conditions and vegetational associations that occurred in the past. Thus, the term “nonanalog” has come into favor to describe this type of species association and will be used herein (Stafford et al., 1999). The generally accepted interpretation for nonanalog faunas during the late Pleistocene is that former habitats and vegetational

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associations also were nonanalog, and thus allowed the coexistence or sympatry of species, generally small mammals, that are not known to co-occur today (Graham and Mead, 1987).

Most previous papers on nonanalog faunas have concentrated on small mammals from late Pleistocene cave deposits in the Midwest, Appalachian Mountains, and mountains of the arid Southwest. These three regions of North America experienced different climatic conditions during the late Pleistocene, and thus have different patterns of nonanalog species associations. In the Midwest, many late Pleistocene cave deposits are found near the southern terminus of the Wisconsinan glacier. Most of the nonanalog species in these sites consist of rodents or shrews now found in tundra or boreal forest habitats that occurred far south of their current ranges, in association with temperate species of small mammals that still live in the general vicinity of the cave sites. For example, late Pleistocene deposits from Peccary Cave in northwestern Arkansas record the presence of several small mammals now restricted to tundra or boreal habitats, including (Semken, 1984; Stafford et al., 1999): Yellow-cheeked Vole *Microtus xanthognathus,* Heather Vole *Phenacomys intermedius*, and Northern Bog Lemming *Mictomys borealis*. Presumably, these species were pushed southward into boreal habitats near the glacial edge, as the region they currently inhabit was covered by glaciers.

There is a strong tendency in southwestern late Pleistocene faunas for small mammals to occur farther south and at lower elevations than present, presumably in response to cooler summer temperatures and greater available moisture during the late Wisconsinan. For example, a number of species of mammals now found in the Rocky Mountains of northern New Mexico occur in late Pleistocene cave faunas at much lower elevations in southern New Mexico where they are no longer found, including (Harris, 1993): Yellow-bellied Marmot *Marmota flaviventris*, Northern Pocket Gopher *Thomomys talpoides*, Bushy-Tailed Woodrat *Neotoma cinerea*, and Mountain Cottontail *Sylvilagus nuttallii*. These and other nonanalog species of mammals occur in late Pleistocene cave faunas in the Guadalupe Mountains of southern New Mexico, together with small mammals typical of Chihuahuan desert grassland habitats found in this region today (Harris, 1993).

Nonanalog associations of birds also are known from numerous late Pleistocene cave faunas in western North America (see review by Brasso and Emslie, 2006) that also show considerable movement by species to the south and to lower elevations than today. As with mammals, species of boreal and tundra habitats are often found in assemblages with those of more temperate and warmer climates. One of the most dramatic examples of this is at Little Box Elder Cave, Wyoming, which produced fossils of Snowy Owl *Nyctea scandiaca*, Boreal Owl *Aegolius funereus*, Hawk Owl *Surnia ulula*, Gyrfalcon *Falco rusticolus*, and White-tailed Ptarmigan *Lagopus* cf. *L. leucurus*, all of which are found in boreal forest and tundra today, in association with more temperate and subtropical species including the extinct Old World vulture *Neophrontops americanus*, Crested Caracara *Caracara cheriway*, Prairie Falcon *Falco mexicanus*, and Greater Sage-grouse *Centrocercus urophasianus* (Emslie, 1985). Several sites in New Mexico (Sandia Cave, Shelter Cave) also have produced *A. funereus* in association with vultures (including California Condor *Gymnogyps californianus*) and *C. urophasianus*. The patterns in all of these cave faunas suggest that a common community representing a steppe-tundra habitat existed over broad regions of western North America during the late Pleistocene (Brasso and Emslie, 2006).

There are two distinct biogeographic patterns evident in nonanalog faunas from late Pleistocene cave deposits in the Appalachian Mountains. The first pattern is very similar to that described above for midwestern faunas, temperate species found in association with now-allopatric arctic or boreal mammals. The second pattern involves species typical of grassland habitats in the midwestern and western U.S. that occur much farther east than their current ranges, in association with species typical of eastern deciduous forest habitats. Examples of extralimital western mammals in Appalachian late Pleistocene faunas include American Badger *Taxidea taxus*, Plains Pocket Gopher *Geomys bursarius*, and Thirteen-lined Ground Squirrel *Spermophilus tridecemlineatus*. All three of these species have been found in New Trout Cave, West Virginia, in association with many species of mammals still found in the vicinity of the cave (McDonald, 2002). Several western birds, including the Black-billed Magpie *Pica pica* and the Greater Prairie Chicken *Tympanuchus cupido*, occurred in Appalachia in the late Pleistocene far outside their modern ranges (Parmalee, 1992).

In addition to the warm temperate fauna that occurs in Florida at present and throughout the Ice Age, the primary geographic influences in Florida Pliocene and Pleistocene faunas are from more arid regions in western North America and tropical regions in Mexico and Central America, not from north temperate or boreal regions (Webb and Wilkins, 1984; Emslie, 1998; Morgan, 2002). Species now restricted to arid habitats in the western U.S. occurred in the Florida peninsula, where they were found in association with species now typical of the Gulf and Atlantic coastal plains. At the same time these western species spread eastward, there is also a fairly diverse fauna of birds and mammals in Florida typical of tropical habitats in Mexico and Central America. Tropical species found in Florida Ice Age faunas are only rarely documented elsewhere in temperate North America. It is not coincidental that many of the same fossil sites in Florida that contain extralimital and/or extinct species of tropical birds and mammals also have species with western affinities; both biogeographic patterns appear to be correlated with glacial intervals.

2. Methods

This paper focuses exclusively on nonanalog or disharmonious vertebrate faunas from Florida, whereas most previous studies have concentrated on nonanalog faunas from the Midwest, Southwest, or Appalachians (e.g., Stafford et al., 1999). It examines several types of nonanalog faunas, including influences from the western United States, Middle America, and the West Indies, as well as species associations that appear to be closely related to sea level changes. The study encompasses birds and mammals, although it also mentions several reptiles. Most previous papers have focused on small mammals, primarily rodents and insectivores. Finally, the analysis covers faunas spanning the past 2.5 million years, from the late Pliocene through the late Pleistocene, whereas most previous studies of nonanalog faunas have concentrated on the late Pleistocene. The approach involves some speculation regarding the biogeography and paleoecology of extinct species of birds and mammals for which there are no direct data on their habitat preferences and only fossil data for their distribution. In these cases, the geographic distribution and ecology of their closest living relatives are used as evidence to interpret records of these species from the Pliocene and/or Pleistocene of Florida.

Birds and bats rarely have been included in studies of nonanalog faunas, presumably because in the opinion of some workers their ability to fly and tendency for many species to migrate long distances diminishes their usefulness in biogeographic studies. The authors strongly disagree with this notion, and instead suggest that fossil birds and bats may be just as informative as small terrestrial or nonvolant mammals in studies of biogeography and nonanalog faunas. Most of the extralimital birds and bats discussed are nonmigratory and have well-defined modern ranges that do not include Florida.

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Most of the fossils discussed in this paper are housed in the vertebrate paleontology collection of the Florida Museum of Natural History (FLMNH), University of Florida, Gainesville, Florida. FLMNH paleontologists have developed a system for naming fossil deposits in Florida that involves numbering individual quarries (originally using roman numerals and now arabic numerals) and assigning a letter designation for separate deposits within a quarry. This system is used primarily for paleokarst deposits in commercial quarries where sites of different age are often located in close proximity. For example, Haile 7C would be the third fossil deposit named within Haile Quarry number 7 (there are more than 20 separate limerock quarries in the Haile Quarry complex in Alachua County). Most of the Florida sites discussed in this paper have been screenwashed for microvertebrates. Sites collected from the 1950s through the mid 1970s were washed through standard window screen (16 mesh, 1.5 mm opening); sites collected after 1975 were screenwashed through both standard window screen and finer mesh brass screen (24 mesh, 1 mm opening). Officially recognized common names for living species are capitalized and follow standard references for birds (AOU, 1983) and mammals (Wilson and Reeder, 2005). For the most part, both the common and scientific names are used for the first time when the species appears in the text. Thereafter, only the scientific name is used.

Abbreviations used in the text are as follows: Great American Biotic Interchange (GABI), Local Fauna (LF), North American land mammal age (NALMA), Mega anna or millions of years before present (Ma), kilo anna or thousands of years before present (ka), radiocarbon years before present (yr BP) when citing radiocarbon (^{14}C) dates.

3. Chronology

The Florida vertebrate fossil sites discussed date to the Ice Age, with ages ranging from the late Pliocene (~2.5 Ma) through late Pleistocene (10 ka). Although the term "Ice Age" is imprecise and often misused in the popular literature, it is useful because non-analog faunas appear to be inherently related to climatic changes associated with the glacial–interglacial cycles of the Ice Age. The modern concept of the Ice Age begins with the first formation of continental glaciers in the Northern Hemisphere at about 2.5 Ma. Thereafter, about 25 glacial–interglacial intervals are documented throughout the remainder of the Pliocene and Pleistocene on approximately a 100 ka cycle.

A recent decision by the International Commission on Stratigraphy and several papers (e.g., Walker and Geissman, 2009) advocate a change in the Pliocene–Pleistocene boundary from about 1.8 Ma (boundary used in this paper) to about 2.6 Ma. Because this boundary change is controversial (e.g., Van Couvering et al., 2009) and the supporting data had not yet been formally published at the time of writing, this paper uses the previous definition for the Pliocene–Pleistocene boundary at 1.8 Ma. This change would affect the age of several faunas discussed in this paper. The late Blancan Haile 7C and Haile 7G LFs and Inglis 1A and Inglis 1C LFs are between 1.8 and 2.2 Ma and are here considered late Pliocene, but would be early Pleistocene under the newly proposed boundary.

The last 2.5 million years can be divided into three North American land mammal ages (NALMA), Blancan, Irvingtonian, and Rancholabrean (Bell et al., 2004). The Blancan covers the interval from 1.8 to 4.9 Ma, only the youngest portion of which in the late Pliocene (~1.8–2.5 Ma) is included within the Ice Age and discussed here. As noted above, under the newly proposed definition of the Pliocene–Pleistocene boundary (Walker and Geissman, 2009), all Florida late Blancan sites would be considered early Pleistocene in age rather than late Pliocene. The Irvingtonian is early to medial Pleistocene in age (~0.25–1.8 Ma) and the Rancholabrean is medial to late Pleistocene (10–250 ka). This paper follows the biochronology for Florida Pliocene and Pleistocene faunas proposed by Morgan and Hulbert (1995), with a few minor exceptions. The oldest sites discussed in this paper are latest Blancan in age (~1.8–2.2 Ma), including the Haile 7C LF and the slightly younger Inglis 1A and Inglis 1C LFs. Morgan and Hulbert (1995) considered Haile 7C to be latest Blancan (~2.0–2.2 Ma) but they placed Inglis 1A in the early Irvingtonian. However, Inglis 1A contains several genera (*Chasmaporthetes*, *Trigonictis*) and species (*Megalonyx leptostomus*, *Ondatra idahoensis*, *Sigmodon curtisi*) of mammals restricted to Blancan faunas in western North America, indicating that Inglis 1A is latest Blancan (~1.8–2.0 Ma; Morgan, 2005).

The Haile 16A LF is considered to be earliest Irvingtonian (~1.6–1.8 Ma). Although Haile 16A lacks *Mammuthus*, the genus most characteristic of Irvingtonian faunas (Morgan and Lucas, 2003; Bell et al., 2004), the absence of mammoths from this site is more likely a taphonomic factor typical of Florida paleokarst faunas (Morgan and Hulbert, 2008). Another Irvingtonian indicator, the arvicoline rodent *Microtus*, does occur at Haile 16A (Martin, 1995), and the presence of *Megalonyx wheatleyi*, *Sigmodon libitinus*, *Erethizon dorsatum*, and *Palaeolama mirifica* is also typical of Florida early Irvingtonian faunas (Morgan and Hulbert, 1995). The Coleman 2A LF is considered late Irvingtonian based on the presence of *Arctodus pristinus*, *Canis armbrusteri*, and *Sigmodon bakeri* (Martin, 1974a; Morgan and Hulbert, 1995).

Although the presence of *Bison* typifies the Rancholabrean (Bell et al., 2004), this genus is often absent in Florida late Pleistocene paleokarst faunas. Florida Rancholabrean faunas are also characterized by the first appearance of the large extinct carnivores *Canis dirus* and *Tremarctos floridanus* and the extant rodents *Oryzomys palustris* and *Sigmodon hispidus* (Morgan and Hulbert, 1995; Morgan, 2002). Because of the humid climate, acidic soils, and other adverse factors, very few Florida late Pleistocene faunas have yielded reliable radiocarbon dates despite repeated efforts (Emslie and Morgan, 1995; Emslie, 1998). The only Florida faunas with good radiocarbon dates are from underwater, such as the Page-Ladson site in the Aucilla River in the eastern Panhandle (Webb and Simons, 2006).

4. Fossil sites

Florida has several hundred late Pliocene and Pleistocene vertebrate faunas ranging in age from about 11 ka to 2.5 Ma. For analysis, 12 sites that each contain several examples of extralimital and/or extinct species of birds and/or mammals with either western or tropical affinities were selected (Fig. 1). These sites encompass most of the late Pliocene and Pleistocene, cover much of the peninsula, and contain diverse samples of small vertebrates, particularly birds and mammals. All of these sites have been carefully excavated and the sediments screenwashed, resulting in a reasonably complete list of the fauna. Below, brief descriptions of these sites are provided, focusing on species with western and tropical affinities. Original descriptions of the localities (see citations under individual sites) and several review papers on Florida Plio-Pleistocene faunas (Morgan and Hulbert, 1995, 2008; Emslie, 1998) provide more detailed information on the geology and associated faunas from the various sites.

4.1. Late Pliocene (late Blancan)

The Haile 7C LF (~2.0–2.2 Ma) was derived from clays and sands filling a sinkhole developed in Eocene limestone located in a commercial limerock mine in Alachua County, northern Florida (Fig. 1, site 1). The site appears to have been a sinkhole pond in the

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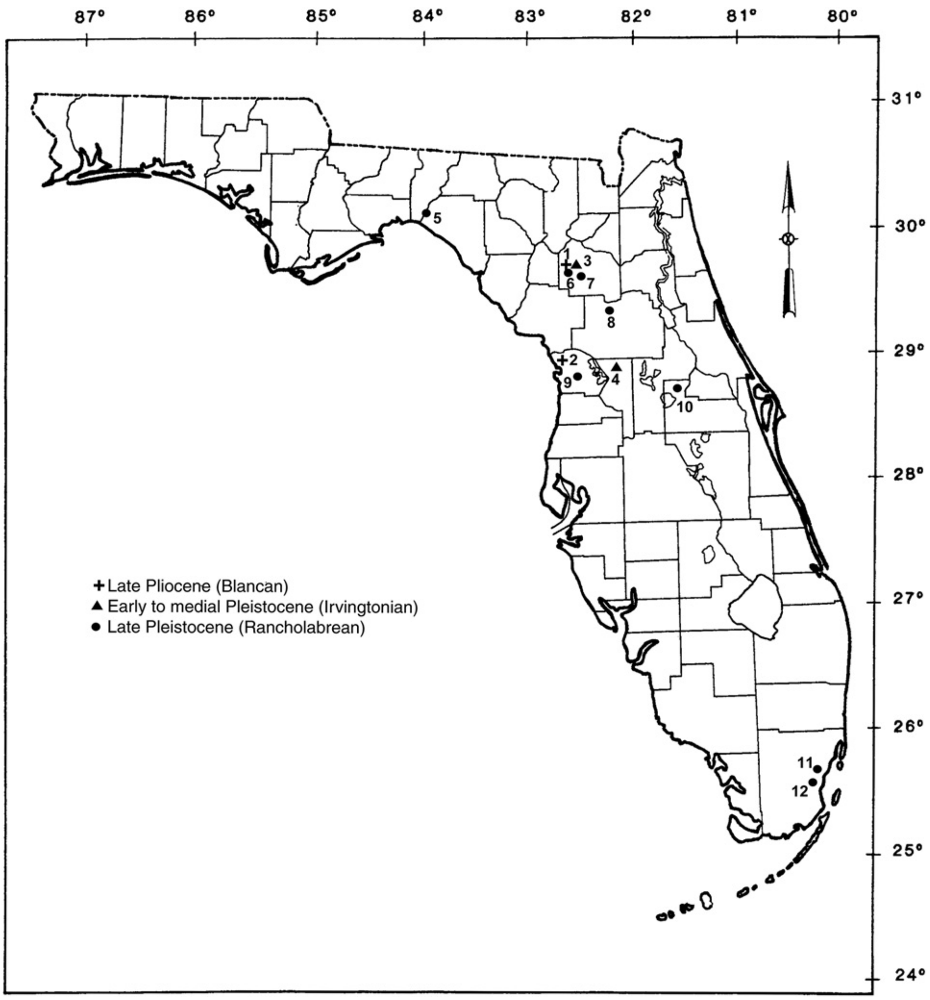

Fig. 1. Map of Florida showing the location of 12 Pliocene and Pleistocene sites discussed in the text that contain significant faunas of birds and mammals with western and/or tropical affinities. Symbols denote different time periods: plus—late Pliocene (Blancan); triangle—early and medial Pleistocene (Irvingtonian); circle—late Pleistocene (Rancholabrean). The numbered sites are listed from oldest (Blancan) to youngest (Rancholabrean) and within a land mammal age from north to south. Blancan: 1. Haile 7C and Haile 7G, Alachua County; 2. Inglis 1A and Inglis 1C, Citrus County. Irvingtonian: 3. Haile 16A, Alachua County; 4. Coleman 2A, Sumter County. Rancholabrean: 5. Aucilla River, Jefferson County; 6. Haile 11B, Alachua County; 7. Arredondo 2A, Alachua County; 8. Reddick 1, Marion County; 9. Lecanto 2A, Citrus County; 10. Rock Springs, Orange County; 11. Cutler Hammock, Dade County; 12. Monkey Jungle Hammock, Dade County.

late Pliocene and is dominated by shells of freshwater turtles and skeletons of large Interchange mammals with Neotropical affinities, including the giant ground sloth *Eremotherium eomigrans*, the pampathere *Holmesina floridanus*, and an undescribed species of the tapir *Tapirus* (Morgan and Hulbert, 1995; Hulbert, 1997; De Iuliis and Cartelle, 1999). Among small mammals there is a single species of Neotropical origin, the extinct porcupine *Erethizon poyeri*, known only from Haile 7C and the nearby Haile 7G (Hulbert, 1997; Hastings et al., 2006). Emslie (1998) identified the Ringed Kingfisher *Ceryle torquata* from Haile 7C, a Neotropical species now found in Middle and South America north to southern Texas. *Amplibuteo concordatus*, an extinct tropical hawk-eagle from Haile 7C, also appears to have Neotropical as well as western affinities (Emslie and Czaplewski, 1999). A large extinct genus and species of condor, *Aizenogyps toomeyae*, is known only from Haile 7C, but the condor lineage extends back to the middle Miocene of California (Emslie, 1988, 1998). Fragmentary fossils of condor referred to *Gymnogyps* sp. from Inglis 1A and from the similar-aged Macasphalt Shell Pit, together with *A. toomeyae*, represent the earliest records of condors from the eastern United States. This group probably evolved in western North America (Emslie, 1988), then followed coastlines and habitat corridors to spread southward and eastward from there, first appearing in South America by the late Miocene (Stucchi, 2008) and Florida by the late Pliocene.

The Inglis 1A and Inglis 1C LFs (∼1.8–2.0 Ma) are fissure deposits exposed in the banks of the now-defunct Cross-Florida Barge Canal near Inglis in Citrus County, about 8 km inland from the Gulf of Mexico (Fig. 1, site 2). Both sites consist of layers of clay and sand filling paleokarst features developed in Eocene limestone. Inglis 1A has a remarkably diverse vertebrate fauna numbering over 150 species, including: 6 anurans (Meylan, 2005); 31 squamate reptiles (Meylan, 1982); several species of turtles and tortoises; 62 birds (Emslie, 1998); and 53 mammals (Webb and Wilkins, 1984; Morgan, 1991; Morgan and Hulbert, 1995). The fossiliferous sediments in the solution feature occur as much as 5 m below current sea level, yet the Inglis 1A fauna lacks marine species suggesting the site formed during a glacial period characterized by low sea level.

Inglis 1A has a diverse nonanalog fauna, including reptiles, birds, and mammals that have affinities with species from the western United States or tropical Middle America. Meylan (1982) identified the alligator lizard *Gerrhonotus* and the western hognose snake *Heterodon nasicus* from Inglis 1A, both of which are now restricted to western North America. The avifauna contains

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a number of species with western affinities, including an extinct Old World vulture *Neophrontops slaughteri*, a condor (*Gymnogyps* sp.), an extinct golden eagle *Aquila bivia*, two species of the pygmy owl *Glaucidium*, the Burrowing Owl *Athene cunicularia*, and the Florida Scrub-jay *Aphelocoma coerulescens* (an endemic species only recognized as systematically distinct from western congeners in 1995; AOU, 1995), and two birds now restricted to the Neotropics, the Least Grebe *Tachybaptus dominicus* and the Great Black Hawk *Buteogallus urubitinga* (Emslie, 1998; Emslie and Czaplewski, 1999). The giant flightless bird *Titanis walleri*, a species of South American origin that was a participant in the Interchange, also occurs in Inglis 1A (Chandler, 1994; Emslie, 1998; Gould and Quitmyer, 2005; MacFadden et al., 2007). Among small mammals, the jackrabbit *Lepus* and the pallid bat *Antrozous* are both now restricted to western North America (Webb and Wilkins, 1984; Morgan, 1991). The small extinct antilocaprid *Capromeryx* is primarily a western genus, but is common at Inglis 1A (Morgan and Hulbert, 1995). The pocket gopher *Orthogeomys propinetis* appears to be Neotropical in origin (Ruez, 2001). Inglis 1A has a remarkable diversity of mammals of South American origin that participated in the GABI, all of which are extinct, including the armadillo *Dasypus bellus*, the pampathere *H. floridanus*, the glyptodont *Glyptotherium arizonae*, the ground sloths, *M. leptostomus*, *Paramylodon harlani*, and *E. eomigrans*, the vampire bat *Desmodus archaeodaptes*, the porcupine *Erethizon kleini*, and the capybara *Hydrochoerus holmesi* (Morgan, 2005).

Inglis 1C has a more limited sample of western and tropical vertebrates, but with some important additions to the vertebrate fauna compared to Inglis 1A. Inglis 1C has produced taxa with both western and Neotropical affinities including the extinct eagle *A. concordatus* that also is represented at Inglis 1A and Duncan, Arizona (Emslie, 1998). The pygmy mouse *Baiomys* and the extinct cormorant *Phalacrocorax idahensis* are restricted to western North America, while *O. propinetis* has Neotropical affinities (Emslie and Czaplewski, 1999; Ruez, 2001). Moreover, many of the birds represent a different environmental setting than that of the slightly older Inglis 1A locality, especially with regard to songbirds that are associated today with dense-scrub habitat (e.g., Northern Cardinal *Cardinalis cardinalus*, Gray Catbird *Dumetella carolinensis*, and four species of thrush including two unidentified species of *Turdus* that may represent species with Neotropical affinities).

4.2. Early and medial Pleistocene (Irvingtonian)

Haile 16A is an early Irvingtonian site from the Haile Quarry complex in Alachua County (Fig. 1, site 3). The fossils were derived from clays filling a karst solution feature developed in Eocene limestone. Haile 16A contains an intriguing nonanalog fauna composed of western species, tropical forms, and several taxa that appear to have northern affinities, together with typical warm temperate species. The site also has a diverse fauna of Interchange mammals, including *D. bellus*, the armadillo *Pachyarmatherium leiseyi*, *H. floridanus*, the ground sloths *M. wheatleyi*, *P. harlani*, and *E. eomigrans*, *D. archaeodaptes*, and the oldest record of the living porcupine *E. dorsatum*. Among small mammals the geomyid *O. propinetis* also has Neotropical affinities, as do two birds, the Gray-breasted Crake *Laterallus exilis* and a chachalaca (family Cracidae) possibly representing an undescribed genus and species (Emslie, 1998). The extinct condor *Gymnogyps kofordi* has western affinities (Emslie, 1988, 1998). Two mammals of northern origin are also known from Haile 16A, the jumping mouse *Zapus* (Morgan and Hulbert, 1995) and the extinct bog lemming *Synaptomys morgani* (Martin et al., 2003).

Coleman 2A is a late Irvingtonian fauna from a limerock mine near Coleman in Sumter County (Fig. 1, site 4). The fauna was derived from a sediment-filled sinkhole of paleokarst origin developed in Eocene limestone (Martin, 1974a). There are 40 species of mammals from the Coleman 2A LF (Martin, 1974a; Webb and Wilkins, 1984) and 32 species of birds (Ritchie, 1980). There is a strong western influence, with records of the Golden Eagle *Aquila chrysaetos* and the Black-billed Magpie *P. pica* (Ritchie, 1980; Emslie, 1998), and three genera of mammals, *Lepus*, the ground squirrel *Spermophilus*, and the smooth-toothed pocket gopher *Thomomys* (Martin, 1974a; Webb and Wilkins, 1984). Tropical taxa at Coleman 2A are primarily represented by Interchange mammals, including the oldest record of the Virginia Opossum *Didelphis virginiana*, as well as the hog-nosed skunk *Conepatus* (Martin, 1974a).

4.3. Late Pleistocene (Rancholabrean)

There are several hundred Rancholabrean faunas distributed throughout the Florida peninsula, a number of which document species of birds and mammals now restricted to western North America or tropical Middle America. Eight Rancholabrean sites with nonanalog faunas containing extralimital and/or extinct species of birds and mammals with western or tropical affinities were selected (Fig. 1), most of which consist of caves, fissures, or sinkholes of paleokarst origin (Morgan and Hulbert, 2008).

The Aucilla River is located in Jefferson County in northwestern peninsular Florida where the panhandle and peninsula meet (Fig. 1, site 5). The late Rancholabrean vertebrate fauna from the Aucilla River was collected from a karst deposit that is now underwater, derived from both the river bottom and in-place sediments. There are associated radiocarbon dates from bone and wood ranging from 11,240 to 18,580 yrBP, although most of the vertebrate fossils are 11–13 ka in age (Webb, 1974; Webb and Simons, 2006). There are two extralimital species with western affinities, the California Condor *G. californianus* and the extant porcupine *E. dorsatum*. Although the porcupine also inhabits northern coniferous forests, this species appears to have invaded Florida from the west during the late Pleistocene. The Margay *Leopardus wiedii* (considered an extinct species *L. amnicola* by some authors) is the only living extralimital Neotropical species from the Aucilla River (Gillette, 1976). Several extinct species from the Aucilla River have tropical affinities, including giant land tortoise *Hesperotestudo crassiscutata*, pampathere *Holmesina septentrionalis*, glyptodont *Glyptotherium floridanum*, bear *T. floridanus*, capybara *H. holmesi*, and tapir *Tapirus veroensis* (Webb and Simons, 2006).

Late Pleistocene caves, fissures, and sinkhole pond deposits are common in the Haile and Arredondo quarries in Alachua County in the northern peninsula, numbering well over 50 individual sites (Morgan and Hulbert, 2008). All of these of deposits occurred in paleokarst and were discovered through commercial limerock mining operations. Two sites in particular, Haile 11B (Fig. 1, site 6) and Arredondo 2A (Fig. 1, site 7), have significant samples of species with western and tropical affinities. Birds with western affinities from Haile 11B include Greater Prairie Chicken *T. cupido*, *A. cunicularia*, *P. pica*, *A. coerulescens*, and the extinct cowbird *Pandanaris floridana*, whereas Crested Caracara *C. cheriway*, *L. exilis*, Southern Lapwing *Vanellus chilensis*, and the extinct hangnest *Cremaster tytthus* have Neotropical affinities (Ligon, 1965; Emslie, 1998). *C. cheriway*, *A. cunicularia*, and *A. coerulescens*, still live in Florida; the rest of the species are extirpated or extinct. The extinct vampire bat *Desmodus stocki* and extinct armadillo *D. bellus* are the only mammals from Haile 11B with Neotropical affinities; there are no western mammals present.

A. coerulescens is the only bird with western affinities from Arredondo 2A; tropical species include the Yellow-headed Caracara *Milvago chimachima*, *V. chilensis*, and *C. tytthus* (Brodkorb, 1959; Emslie, 1998). The only Florida record of the Ruffed Grouse *Bonasa*

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umbellus, a northern species no longer found in Florida, is from the adjacent Arredondo 1 site (Brodkorb, 1959). The mammalian fauna includes the extinct pocket gopher *Thomomys orientalis* of western origin and the extinct Neotropical bat *D. stocki* (Webb and Wilkins, 1984). A large extinct chipmunk *Tamias aristus* is a rare northern element from Arredondo 2A (Webb and Wilkins, 1984).

The Reddick 1 Fauna was collected from an abandoned limerock quarry near Reddick in Marion County (Fig. 1, site 8). The fossils were derived from stratified clays and sands that fill caverns and solution pipes in Eocene limestone. Reddick 1 has one of the most abundant and diverse vertebrate faunas of any Rancholabrean site in Florida with over 160 species: 9 amphibians, 32 reptiles, 64 birds, and 56 mammals (Brodkorb, 1957; Auffenberg, 1963; Gut and Ray, 1963; Hamon, 1964; Webb and Wilkins, 1984). The large number of species with western and tropical affinities is related both to the deposition of the site during the Wisconsinan glacial and the incredibly diverse, well-sampled fauna of small terrestrial vertebrates. Literally tons of sediment from this site have been sampled for microvertebrates since the inception of screenwashing in the 1950s. Birds with western affinities from Reddick 1 include the extinct teratorn *Teratornis merriami*, *G. californianus*, *A. cunicularia*, *P. pica*, and the extinct *P. floridana*; tropical birds include *C. cheriway*, *M. chimachima*, and *L. exilis* (Brodkorb, 1957; Emslie, 1998). Tropical mammals consist of *D. stocki*, Ocelot *Leopardus pardalis*, and Eastern Hog-nosed Skunk *Conepatus leuconotus* (Gut, 1959; Ray et al., 1963; Webb and Wilkins, 1984; Morgan, 1991), as well as several Interchange mammals, including *D. bellus*, *H. septentrionalis,* and *H. holmesi*. There are no mammals with western affinities from Reddick 1.

The Lecanto 2A LF from Citrus County along the central Gulf Coast (Fig. 1, site 9) has a diverse nonanalog fauna of both western and tropical species of birds and mammals, together with one northern form, associated with many species typical of Florida and the southeastern coastal plain (Morgan, 1991; Emslie, 1998). The fossils were derived from a fissure deposit of paleokarst origin developed in Eocene limestone. Taxa from Lecanto 2A with western affinities include the Band-tailed Pigeon *Columba fasciata*, *P. pica*, Great-tailed Grackle *Quiscalus mexicanus*, and the extinct pocket gopher *T. orientalis*. Neotropical species include the Northern Jacana *Jacana spinosa*, *L. exilis*, and Underwood's Mastiff Bat *Eumops underwoodi* (Morgan, 1991; Emslie, 1998). The Northern Saw-whet Owl *Aegolius acadicus* is a rare extralimital species with northern affinities (Emslie, 1998).

Rock Springs is a submerged cave and associated spring run in Orange County, central Florida (Fig. 1, site 10). Both the birds (Woolfenden, 1959) and mammals (Wilkins, 1983) from Rock Springs have been reviewed. This site records the presence of *Thomomys*, a genus now restricted to western North America, as well as two tropical mammals, Peters' Ghost-faced Bat *Mormoops megalophylla* and the Margay *L. wiedii* (Ray et al., 1963; Gillette, 1976; Wilkins, 1983, 1985). Among the 35 species of birds identified from this site, most represent wetland, aquatic, and riparian habitats and currently occur in Florida (Woolfenden, 1959).

The Cutler Hammock and Monkey Jungle Hammock LFs are sinkhole/cave deposits developed in the Pleistocene Miami Limestone in Dade County, southernmost peninsular Florida (Fig. 1, sites 11, 12). The entire vertebrate fauna from Cutler Hammock is published (Emslie and Morgan, 1995; Emslie, 1998; Morgan, 2002); only the mammals from Monkey Jungle have been studied (Morgan, 1991, 2002). Cutler Hammock was probably used as a den by dire wolves *C. dirus* in the late Pleistocene. The site contains the largest collection of fossils of *C. dirus* in the eastern United States, including teeth of at least 13 young animals, and is the second largest (other than Rancho La Brea) fossil assemblage for this species in North America. Cutler Hammock has a diverse fauna of extinct and extralimital birds, including *G. californianus*, *A. chrysaetos*, and *P. pica* with western affinities and three tropical species, the large extinct anhinga *Anhinga beckeri*, the extinct hawk-eagle *Spizaetus grinnelli*, and *M. chimachima* (Emslie, 1998). This site has one of the few Florida records of the teratorn *T. merriami* (Emslie, 1998), a species primarily found in western North America but originally of South American origin. There are no western mammals from either Cutler Hammock or Monkey Jungle, but there are several mammals with Neotropical affinities, the large carnivores *T. floridanus* and *Panthera onca*, found in both sites, and three bats, including *M. megalophylla*, the extinct mormoopid *Pteronotus pristinus*, and the Florida Mastiff Bat *Eumops floridanus* from Monkey Jungle and *M. megalophylla* from Cutler Hammock (Martin, 1977; Morgan, 1991, 2002; Emslie and Morgan, 1995).

5. Biogeography

5.1. Biogeography of Florida's current bird and mammal faunas

Florida is the southernmost region in the continental United States, extending well into subtropical latitudes (from about 31° N at the border with Alabama and Georgia to about 24°30′ N at Key West). Despite the subtropical climate and vegetation in the southern half of the Florida peninsula, surprisingly few mammals with tropical affinities are currently found in this region, almost all of which are bats (Brown, 1997). There is a considerably larger tropical avifauna in southern peninsular Florida and the Florida Keys, including species with West Indian affinities and species from the continental Neotropics in Mexico and Central America (Robertson and Woolfenden, 1992). The only other regions in the continental United States that support species of Neotropical birds and mammals are the Rio Grande valley of extreme southern Texas and the Sonoran and Chihuahuan deserts of the arid Southwest, including southwestern Texas and the southern portions of California, Arizona, and New Mexico. These areas document the northernmost range extensions of otherwise primarily mainland tropical species, whereas the Florida records represent either disjunct populations of continental Neotropical species or northern range extensions of West Indian species. The Florida peninsula is regarded as a southern extension of the Nearctic biogeographic region because the majority of its modern terrestrial vertebrate fauna is temperate in origin not tropical. However, other studies (e.g., Olson et al., 2001) place southern peninsular Florida in the Neotropical biogeographic region.

A rather diverse fauna of tropical birds occurs in southern peninsular Florida, including both nonmigratory breeding residents and species otherwise endemic to the West Indies. The Snail Kite *Rostrhamus sociabilis*, Short-tailed Hawk *Buteo brachyurus*, and Crested Caracara *C. cheriway* are primarily mainland Neotropical species, with disjunct populations in south Florida. Among these species, only the caracara has a Pleistocene fossil record in Florida. West Indian birds found in the southern peninsula and Keys appear to be recent arrivals from Cuba or the Bahamas and none have a fossil record in Florida, including: White-crowned Pigeon *Columba leucocephala*, Mangrove Cuckoo *Coccyzus minor*, Smooth-billed Ani *Crotophaga ani*, Antillean Nightjar *Chordeiles gundlachi*, Gray Kingbird *Tyrannus dominicensis*, Black-whiskered Vireo *Vireo altiloquus*, and Bahama Mockingbird *Mimus gundlachi*. Two extant birds from peninsular Florida have western affinities and are not found elsewhere in the eastern United States, the Burrowing Owl *A. cunicularia* and Florida Scrub-jay *A. coerulescens*, both of which have been identified from the late Blancan Inglis 1A LF and several Florida Pleistocene faunas (Emslie, 1996, 1998). *A. cunicularia* is widespread in the western

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United States, but also occurs in Mexico, several West Indian islands, and in South America. *A. coerulescens* has been endemic to Florida since at least the late Pliocene (Emslie, 1996).

The modern mammals of Florida are typical of the warm temperate fauna found throughout the southeastern United States, with the exception of three tropical bats from the southern peninsula and Florida Keys, the Florida Mouse *Podomys floridanus*, and the Round-tailed Muskrat *Neofiber alleni* (Hamilton and Whitaker, 1979; Brown, 1997). Two Neotropical bats have been reported from the Florida Keys, the Jamaican Fruit-eating Bat *Artibeus jamaicensis* and Pallas' Mastiff Bat *Molossus molossus* (Frank, 1997a,b). These are the only records of these two bats from the United States, neither of which is known in Florida Pleistocene fossil deposits (Morgan, 1991). *A. jamaicensis* and *M. molossus* appear to be fairly recent immigrants from Cuba, located about 150 km south of the Florida Keys across the Straits of Florida. A third tropical bat from southern Florida, the Florida Mastiff Bat *E. floridanus*, is also unknown elsewhere in temperate North America. Although now considered to be endemic to the southern third of the Florida peninsula (Timm and Genoways, 2004), *E. floridanus* was long regarded as a subspecies of the widespread Neotropical species *E. glaucinus*, found in Cuba and Jamaica and on the mainland from southern Mexico south through Central America and into South America (Koopman, 1971; Eger, 1977). Before being discovered as a living animal in southern peninsular Florida, *E. floridanus* was originally described as a fossil, *Molossides floridanus*, from the Rancholabrean Melbourne LF along Florida's central Atlantic coast (Allen, 1932), and has since been reported from three late Pleistocene and Holocene fossil sites in southeastern peninsular Florida (Martin, 1977; Morgan, 1991). *P. floridanus* is an endemic genus and species of cricetid rodent with Neotropical affinities (Carleton, 1980) that has been restricted to Florida since the early Pleistocene (Morgan and White, 1995). With the exception of a minor range extension northward into the Okeefenokee Swamp in southernmost Georgia, *N. alleni* is also now endemic to Florida, although this species was somewhat more widely distributed outside of Florida in the Rancholabrean (Kurtén and Anderson, 1980). *Neofiber* is an arvicoline rodent with its origins in temperate North America.

5.2. Florida Interchange fauna

Among the extinct species of vertebrates in Florida Pliocene and Pleistocene faunas, those taxa involved in the Great American Biotic Interchange (GABI) constitute the largest group with tropical affinities. Most of these extinct species are large mammals, although at least three large birds and several smaller mammals involved in the GABI are documented in Florida faunas as well (Emslie, 1998; Morgan, 2005). Florida has the most diverse Plio-Pleistocene Interchange fauna in temperate North America. This is almost certainly related to the subtropical climate in the Florida peninsula, coupled with the development of a Gulf Coast savanna corridor that served as a dispersal route between Florida and South America by way of Middle America (Webb, 1974, 1978). Florida late Pliocene and Pleistocene faunas document the presence of 24 extinct species of Interchange mammals and birds of South American origin (Morgan, 2005; species in the same genus separated by "/" are not contemporaneous): giant, flightless, phorusrhacid bird *T. walleri*; teratorns *Aiolornis incredibilis* and *T. merriami*; armadillos *D. bellus* and *P. leiseyi*; pampatheres *H. floridanus*/*H. septentrionalis*; glyptodonts *G. arizonae*/*G. floridanum*; mylodontid ground sloths *Paramylodon* cf. *P. garbanii*/*P. harlani*; megalonychid ground sloths *M. leptostomus*/*M. wheatleyi*/*M. jeffersonii*; megatheriid ground sloths *E. eomigrans*/*Eremotherium laurillardi*; nothrotheriid ground sloth *Nothrotheriops texanus*; vampire bats *D. archaeodaptes*/*D. stocki*; porcupines *E. poyeri*/*E. kleini*; and capybaras *H. holmesi* and *Neochoerus dichroplax*/*Neochoerus pinckneyi*. Not all of these Interchange species occur together in a single site nor are they all found in the same NALMA (Table 1).

The two most diverse Interchange faunas in temperate North America are from Florida, the latest Blancan Inglis 1A (reviewed above) with 10 Interchange species and the early Irvingtonian Leisey Shell Pit with 12 species (Morgan, 2005). Pleistocene sites in Mexico and Central America have Interchange faunas comparable to those of Florida, whereas temperate sites elsewhere in the United States generally contain only a few GABI taxa. Although the species that participated in the GABI are ultimately of South American or Neotropical origin, they do not all have a tropical/subtropical biogeographic distribution in North America. For example, during the Irvingtonian and Rancholabrean, *Paramylodon*, *Megalonyx*, and *Erethizon* are widespread throughout North America, but are more typical of temperate regions. In addition to these extinct species, two living Interchange mammals are found in Florida Pleistocene sites, the opossum *D. virginiana* and the porcupine *E. dorsatum*. The porcupine is currently extralimital to Florida.

The Gulf Coast savanna corridor helps explain why certain tropical/subtropical taxa are present in Rancholabrean faunas in Middle America, Florida, and elsewhere on the Atlantic and Gulf coastal plains in the southeastern United States, but are absent in sites of similar age in western North America. Among large mammals, this Florida/Middle America connection in the Rancholabrean includes at least four Interchange species or species pairs (for species pairs, Florida species is listed first, separated by "/" from the species found in Middle America): glyptodonts (*G. floridanum*/*G. mexicanum*), pampatheres (*H. septentrionalis*), giant ground sloth (*E. laurillardi*), and giant capybara (*N. pinckneyi*/*N. robustus*). The gompthothere *Cuvieronius tropicus* also seems to fit this same distributional pattern in the Rancholabrean, although this genus or its progenitor originated in North America and migrated to South America during the Interchange. Apparently, the climate in the southwestern United States during the late Pleistocene was too dry, too cold, or perhaps a combination of these two factors, and could not support tropical to subtropical members of the Interchange fauna. This hypothesis is supported by the occurrence of *Glyptotherium* and *Neochoerus* in the southwestern United States in the late Blancan (Morgan, 2008), during a time period when the climate in this region was characterized by warmer temperatures and more precipitation (Thompson, 1991). Cooler temperatures probably limited the northward range of these species in eastern North America.

5.3. Biogeography of Florida Plio-Pleistocene birds

Many of the extralimital and extinct species of birds from Florida Plio-Pleistocene faunas are either of tropical or western origin, although there are a few species with northern affinities. Three birds in the tropical component are South American in origin and thus members of the Interchange fauna, *T. walleri* and the teratorns *A. incredibilis* and *T. merriami* (Brodkorb, 1963; Campbell and Tonni, 1981; Emslie, 1998). Extralimital or extirpated species of extant Neotropical birds in Florida Plio-Pleistocene faunas include (Emslie, 1998; Table 1): five birds typical of tropical wetlands, Least Grebe *T. dominicus*, Greater Flamingo *Phoenicopterus ruber*, Gray-breasted Crake *L. exilis*, Northern Jacana *J. spinosa*, and Ringed Kingfisher *C. torquata*; and three species found in tropical grasslands or forests, Great Black Hawk *B. urubitinga*, Yellow-headed Caracara *M. chimachima*, and Southern Lapwing *V. chilensis*. There are also several extinct birds of tropical origin, including a chachalaca (Family Cracidae), two hawk-eagles *A. concordatus* and *S. grinnelli*, a jay *Henocitta brodkorbi*, and a hangnest *C. tytthus*. Two species of

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Table 1

Extinct and extralimital species of birds and mammals with tropical and western affinities from the late Pliocene (late Blancan) and Pleistocene (Irvingtonian and Rancholabrean) of Florida. For each species, the biogeographic affinities, Florida sites where they occur (including the age, B = Blancan; I = Irvingtonian; R = Rancholabrean; E = early; M = medial; L = late), and references are provided. Only key sites are listed for species that occur in a large number of Florida localities. Several species of birds and mammals on this list occur in both tropical Middle America and western North America; their biogeographic affinities are given as tropical/western. Species listed as tropical/GABI were involved in the Great American Biotic Interchange and are ultimately of South American origin, although some of these species are also widespread in western North America.

Species	Biogeographic affinity	Sites and age	References
Birds			
Gavia pacifica	Western	Inglis 1A (LB)	Emslie, 1998
Tachybaptus dominicus	Tropical	Inglis 1A (LB); Payne Creek Mine (EI)	Steadman, 1984; Emslie, 1998
Phalacrocorax idahensis[a]	Western	Inglis 1C (LB)	Emslie, 1998
Anhinga beckeri[a]	Tropical	D & M Shell Pit (LB); Leisey Shell Pit 3A (EI) Coleman 3C (R); Cutler Hammock (R)	Emslie, 1998
Ajaia chione[a]	Tropical	Leisey Shell Pit 1A (EI)	Emslie, 1995
Aiolornis incredibilis[a]	Tropical/GABI	Leisey Shell Pit 1A (EI)	Emslie, 1995
Teratornis merriami[a]	Tropical/GABI	Leisey Shell Pit 1A (EI); Reddick 1A (R); Cutler Hammock (R)	Emslie, 1995, 1998
Aizenogyps toomeyae[a]	Western	Haile 7C (LB)	Emslie, 1998
Gymnogyps kofordi[a]	Western	Haile 16A (EI); Leisey Shell Pit 1A (EI)	Emslie, 1988, 1998
Gymnogyps californianus	Western	Aucilla River (R); Reddick 1 (R); Cutler Hammock (R)	Emslie, 1998; Webb and Simons, 2006
Phoenicopterus copei[a]	Tropical/Western	Leisey Shell Pit 1A (EI)	Emslie, 1995
Phoenicopterus ruber	Tropical	Leisey Shell Pit 1A (EI)	Emslie, 1995
Anabernicula gracilenta[a]	Western	Inglis 1A (LB), Leisey Shell Pit 1A (EI)	Speaker Carr, 1981; Emslie, 1995
Branta dickeyi[a]	Western	Leisey Shell Pit 1A (EI)	Emslie, 1995
Neophrontops slaughteri[a]	Western	Inglis 1A (LB)	Emslie, 1998
Buteogallus urubitinga	Tropical	Inglis 1A (LB)	Emslie, 1998
Buteogallus fragilis[a]	Tropical/Western	Pelican Road Shell Pit (LB)	Emslie, 1998
Amplibuteo concordatus[a]	Tropical	Haile 7C (LB); Inglis 1C (LB)	Emslie and Czaplewski, 1999
Amplibuteo woodwardi[a]	Tropical/Western	McLeod (MI); Ichetucknee River (R)	Emslie, 1998
Aquila bivia[a]	Western	Inglis 1A (LB)	Emslie and Czaplewski, 1999
Aquila chrysaetos	Western	Coleman 2A (LI); Cutler Hammock (R)	Ritchie, 1980; Emslie, 1998
Spizaetus grinnelli[a]	Tropical	West Palm Beach (R); Cutler Hammock (R)	Becker, 1985; Emslie, 1998
Milvago chimachima	Tropical	Ichetucknee River (R); Arredondo 2A (R); Reddick 1A (R); Cutler Hammock (R)	Brodkorb, 1959; Campbell, 1980; Emslie, 1998
Cracidae (gen. & sp. indet.)	Tropical	Haile 16A (EI)	Emslie, 1998
Tympanuchus cupido	Western	Haile 11B (R); Surprise Cave (R)	Ligon, 1965; this paper
Laterallus exilis	Tropical	Haile 16A (EI); Haile 11B (R); Reddick 1A (R); Lecanto 2A (R)	Brodkorb, 1952; Olson, 1974; Emslie, 1998
Titanis walleri[a]	Tropical/GABI	Santa Fe 1 (LB); Inglis 1A (LB); Port Charlotte (LB)	Brodkorb, 1963; Chandler, 1994; Emslie, 1998; Gould and Quitmyer, 2005; MacFadden et al., 2007
Vanellus chilensis	Tropical	Arredondo 2A (R); Haile 11B (R)	Brodkorb, 1959; Ligon, 1965
Jacana spinosa	Tropical	Lecanto 2A (R); Leisey Shell Pit 2 (R)	Emslie, 1995, 1998
Columba fasciata	Western	Lecanto 2A (R)	Emslie, 1998
Glaucidium explorator[a]	Tropical/Western	Inglis 1A (LB)	Emslie, 1998
Glaucidium sp.	Tropical/Western	Inglis 1A (LB)	Emslie, 1998
Ceryle torquata	Tropical	Haile 7C (LB)	Emslie, 1998
Pica pica	Western	Coleman 2A (LI); Haile 11B (R); Reddick 1A (R); Lecanto 2A (R), Cutler Hammock (R)	Brodkorb, 1957; Ritchie, 1980; Emslie, 1998
Henocitta brodkorbi[a]	Tropical	Williston (R)	Holman, 1959
Cremaster tytthus[a]	Tropical	Arredondo 2A (R); Haile 11B (R)	Brodkorb, 1959; Ligon, 1965
Pandanaris floridana[a]	Western	Haile 11B (R); Reddick 1A (R)	Brodkorb, 1957; Ligon, 1965
Quiscalus mexicanus	Western	Lecanto 2A (R)	Emslie, 1998
Mammals			
Dasypus bellus[a]	Tropical/GABI	Numerous FL Blancan, Irvingtonian and Rancholabrean sites	Morgan and Hulbert, 1995; Morgan, 2005
Pachyarmatherium leiseyi[a]	Tropical/GABI	~10 FL L. Blancan and *E.* Irvingtonian sites	Downing and White, 1995; Morgan, 2005
Holmesina floridanus[a]	Tropical/GABI	Numerous FL L. Blancan-E. Irvingtonian sites	Hulbert and Morgan, 1993
Holmesina septentrionalis[a]	Tropical/GABI	Numerous FL M. Irvingtonian-Rancholabrean sites	Hulbert and Morgan, 1993
Glyptotherium arizonae[a]	Tropical/Western/GABI	Numerous FL L. Blancan-E. Irvingtonian sites	Gillette and Ray, 1981; Morgan, 2005
Glyptotherium floridanum[a]	Tropical/GABI	Numerous FL Rancholabrean sites	Gillette and Ray, 1981; Morgan, 2005
Paramylodon cf. *P. garbanii*[a]	Tropical/Western/GABI	Haile 15A (LB); Macasphalt Shell Pit (LB)	Robertson, 1976; Morgan and Hulbert, 1995
Eremotherium eomigrans[a]	Tropical/GABI	Numerous FL Blancan and Irvingtonian sites	De Iuliis and Cartelle, 1999; Morgan, 2005
Eremotherium laurillardi	Tropical/GABI	Daytona Beach (R)	Cartelle and De Iuliis, 1995
Nothrotheriops texanus[a]	Tropical/Western/GABI	Leisey Shell Pit 1A (EI); Pool Branch (EI)	McDonald, 1995
Mormoops megalophylla	Tropical	Rock Springs (R); Cutler Hammock (R); Monkey Jungle (R)	Ray et al., 1963; Wilkins, 1983; Morgan, 1991, 2002
Pteronotus pristinus[a]	Tropical	Monkey Jungle (R)	Morgan, 1991
Desmodus archaeodaptes[a]	Tropical/GABI	Inglis 1A (LB); Haile 16A (EI); Haile 21A (EI)	Morgan et al., 1988
Desmodus stocki[a]	Tropical/GABI	Arredondo 2A (R); Haile 1A (R); Reddick 1 (R)	Gut, 1959; Morgan, 1991
Eumops underwoodi	Tropical	Lecanto 2A (R)	Morgan, 1991
Leopardus pardalis	Tropical	Haile 1A (R); Reddick 1 (R)	Ray et al., 1963; Kurtén, 1965

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Table 1 (*continued*)

Species	Biogeographic affinity	Sites and age	References
Leopardus wiedii (=*L. amnicola*[a])	Tropical	Aucilla River (R); Ichetucknee River (R); Waccasassa River (R); Rock Springs (R); Melbourne (R); Merritt Island (R), Nocatee (R)	Ray, 1964; Gillette, 1976; Werdelin, 1985
Panthera onca	Tropical	McLeod (MI); Coleman 2A (LI); numerous FL Rancholabrean sites	Kurtén, 1965; Martin, 1974a; Seymour, 1993
Conepatus leuconotus	Tropical	Haile 7A (R); Williston 3A (R)	Ray et al., 1963
Conepatus robustus[a]	Tropical	Haile 14B (R), Reddick 2C (R)	Martin, 1978
Conepatus sp.	Tropical	Coleman 2A (LI)	Martin, 1974b
Tremarctos floridanus[a]	Tropical	Reddick 1 (R); Devil's Den (R); Rock Springs (R); Cutler Hammock (R), Monkey Jungle (R); numerous other FL Rancholabrean sites	Kurtén, 1966; Webb, 1974; Emslie and Morgan, 1995; Morgan, 2002
Lepus cf. *L. townsendii*	Western	Leisey Shell Pit 1A (EI)	Morgan and White, 1995
Lepus sp.	Western	Inglis 1A (LB); Payne Creek Mine (EI); McLeod (MI); Coleman 2A (LI)	Martin, 1974a; Morgan and White, 1995
Spermophilus sp.	Western	Haile 14A (R); Surprise Cave (R)	Martin, 1974b; this paper
Orthogeomys propinetis[a]	Tropical	Inglis 1A, 1C (LB); Haile 16A (EI)	Wilkins, 1984; Ruez, 2001
Thomomys orientalis[a]	Western	Coleman 2A (LI); Williston 3B (R); Sabertooth Cave Cave (R); Lecanto 2A (R); Rock Springs (R)	Simpson, 1928; Wilkins, 1985
Erethizon poyeri[a]	Tropical/GABI	Haile 7C, 7G (LB)	Hulbert, 1997; Hastings et al., 2006
Erethizon kleini[a]	Tropical/GABI	Inglis 1A (LB)	Frazier, 1981
Erethizon dorsatum	Western/GABI	Aucilla River (R); Waccasassa River (R); New Port Richey (R); Seminole Field (R)	Frazier, 1981; Morgan and White, 1995
Hydrochoerus holmesi[a]	Tropical/GABI	Numerous FL Blancan, Irvingtonian, and Rancholabrean sites	Morgan, 2005
Neochoerus dichroplax[a]	Tropical/GABI	Macasphalt Shell Pit (LB); Mule Pen Quarry (LB)	Ahearn and Lance, 1980; Morgan and Hulbert, 1995
Neochoerus pinckneyi[a]	Tropical/GABI	Numerous FL Rancholabrean sites	Morgan, 2005
Baiomys sp.	Tropical/Western	Inglis 1C (LB)	Ruez, 2001
Tapirus haysii[a]	Tropical	Numerous FL Irvingtonian sites	Hulbert, 1995
Tapirus veroensis[a]	Tropical	Numerous FL Rancholabrean sites	Webb, 1974; Hulbert, 2001
Pecari sp.	Tropical	Peace River (R)	Hulbert et al., 2009

[a] Extinct species.

the pygmy owl *Glaucidium* from Inglis 1A, one extinct and one unidentified, represent the only eastern North American records of this genus (Emslie, 1998). Although there are three living species of *Glaucidium* in western North America, this genus is most diverse in Central and South America and likely originated there (Emslie, 1998). The two species of *Glaucidium* from Inglis 1A are listed as having both tropical and western affinities in Table 1. These birds indicate a biogeographic corridor along the Gulf Coastal plain that had a mixture of forest and open savanna/wetland habitats.

Extralimital species of birds from Florida Pleistocene sites that occur primarily in western North America at present include: Greater Prairie Chicken *T. cupido*, California Condor *G. californianus*, Golden Eagle *A. chrysaetos*, Band-tailed Pigeon *C. fasciata*, Black-billed Magpie *P. pica*, and Great-tailed Grackle *Q. mexicanus*. A number of extinct species of birds from Florida appear to be western in origin as well, including a cormorant *P. idahensis*, a shelduck *Anabernicula gracilenta*, a large goose *Branta dickeyi*, an Old World Vulture *N. slaughteri*, a condor *G. kofordi*, a golden eagle *A. bivia*, and a cowbird *P. floridana* (Emslie, 1998; Emslie and Czaplewski, 1999). Though teratorns are ultimately of South American origin, most records of *Aiolornis* and *Teratornis* are from western North America and Florida (Campbell and Tonni, 1981; Emslie, 1998; Campbell et al., 1999). These birds suggest a biogeographic corridor connecting Florida with western North America existed during the late Pliocene and Pleistocene, consisting of desert grassland/savanna and wetlands habitats.

There are two extralimital birds from the Florida Rancholabrean that now occur far to the north, each known from a single fauna. The Northern Saw-whet Owl *A. acadicus*, a bird typical of northern coniferous forests, was identified from Lecanto 2A (Emslie, 1998). Arredondo 1 contains the Ruffed Grouse *B. umbellus*, now found no farther south than the Appalachian Mountains of northern Alabama and Georgia (Brodkorb, 1959).

The reasonably complete record of birds from the Ice Age of Florida allowed Emslie (1998, 2007) to compare origins and extinctions of various species and communities with climate change. It is apparent that the relatively rapid changes in sea level that occurred in Florida compared to other regions of North America led to many community changes as the Gulf Coast corridor expanded during glacial intervals and contracted or disappeared in interglacials. These climate episodes had a profound influence on community structure in the Florida Peninsula, especially in wetland habitats, that in part explain some of the disjunct distributions found there today.

5.4. Biogeography of Florida Plio-Pleistocene mammals

The majority of mammals with tropical affinities in Florida Plio-Pleistocene sites were participants in the GABI. Most were large extinct mammals and are discussed above. Among smaller mammals, members of the Interchange fauna included the opossum *D. virginiana*, the extinct vampire bats *D. archaeodaptes* and *D. stocki*, the mastiff or bonnetted bats *E. floridanus* and *E. underwoodi*, the extinct porcupines *E. poyeri* and *E. kleini*, and the extant porcupine *E. dorsatum*.

Other extralimital tropical mammals in Florida Plio-Pleistocene faunas consist of carnivores, several additional bats, and a rodent, all of North American ancestry (Table 1). The Neotropical carnivores in Florida Pleistocene faunas are clearly North American in origin. Even though members of the order Carnivora did not enter South America until after its connection with North America at the Panamanian Isthmus in the early Pliocene, there is a rather diverse extant Neotropical carnivore fauna endemic to Central and South America. Some of these species or their progenitors may have inhabited tropical North America prior to the Interchange; however, their fossil record is poor.

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There are four extant species of Neotropical carnivores in Florida Pleistocene sites: two small spotted cats in the genus *Leopardus* (formerly *Felis*), the Ocelot *L. pardalis* and Margay *L. wiedii* (*L. amnicola* of some authors); the Jaguar *P. onca*; and the Eastern Hog-nosed Skunk *C. leuconotus*. There are also two extinct carnivores with tropical affinities, the large hog-nosed skunk *Conepatus robustus* and the Florida cave bear *T. floridanus*. *L. pardalis* has been reported from two Florida Rancholabrean faunas, Haile 1A in Alachua County (Kurtén, 1965) and Reddick 1A in Marion County (Ray et al., 1963). Ray (1964) identified the Jaguarundi *Puma* (formerly *Felis* and *Herpailurus*) *yagouaroundi* from two Florida late Pleistocene sites, Rock Springs and Melbourne in Brevard County on the central Atlantic Coast. However, Gillette (1976) referred these specimens to an extinct species of small cat, *Felis* (=*Leopardus*) *amnicola*, that he described from the Aucilla River in the Florida panhandle. Werdelin (1985) considered *amnicola* to be a subspecies of *L. wiedii*, an extant Neotropical felid, and referred several additional Florida late Pleistocene fossils to this species (Table 1). The ocelot and margay are primarily inhabitants of tropical forests in Middle and South America, although ocelots are known from northeastern Mexico and southern Texas (Hall, 1981).

The earliest records of *P. onca* from Florida are the medial Irvingtonian McLeod LF in Levy County (Seymour, 1993) and the late Irvingtonian Coleman 2A LF in Sumter County (Martin, 1974a). The jaguar is the most common large felid in Florida Rancholabrean faunas where it occurs in more than 30 sites (Kurtén, 1965; Morgan and Seymour, 1997). *P. onca* is fairly widely distributed in Irvingtonian sites as far north as Pennsylvania (Seymour, 1993), but has a more southerly distribution in the Rancholabrean, from Florida north to Tennessee and west to Nevada (Kurtén and Anderson, 1980). Today jaguars are found primarily in tropical forests in Middle and South America, but do occur as far north as the southern parts of Arizona, New Mexico, and Texas.

C. leuconotus has been reported from two Rancholabrean faunas in Florida, Haile 7A in Alachua County and Williston 3A in Levy County (Ray et al., 1963). *C. leuconotus* has a primarily Neotropical distribution at the present time, occurring from the Gulf coastal lowlands of Mexico in the states of Veracruz and Tamaulipas north to southernmost Texas (Hall, 1981). The other living species of *Conepatus* found in the United States, *C. mesoleucus*, is also found primarily in Mexico but does occur northward into the southwestern United States (Hall, 1981). An unidentified species of *Conepatus* was reported from Coleman 2A (Martin, 1974a). Martin (1978) described a large extinct species of hog-nosed skunk, *C. robustus*, from two Florida Rancholabrean faunas, Haile 14B in Alachua County and the Reddick 2C in Marion County. Like other members of the genus *Conepatus*, *C. robustus* was probably Neotropical in origin.

The extinct Florida cave bear *T. floridanus* is one of the most common large carnivores in Florida Rancholabrean faunas, including several skeletons from the Devil's Den LF, an underwater cave site in Levy County (Kurtén, 1966; Martin and Webb, 1974). This bear also occurs as far north as Georgia and Tennessee, on the Gulf Coastal Plain of Texas, and south to Mexico and Belize (Kurtén and Anderson, 1980; Czaplewski et al., 2003). The genus *Tremarctos* is now restricted to South America where the only living species, the Spectacled Bear *T. ornatus*, is found in the Andes Mountains from Colombia and Venezuela south to Peru and Bolivia. Tremarctine bears evolved in North America. The earliest member of the subfamily is the genus *Plionarctos* from the early Pliocene, including specimens from the latest Hemphillian Palmetto Fauna in central Florida (Webb et al., 2008). Tremarctines first reached South America in the early Pleistocene as participants in the GABI.

Among Florida Plio-Pleistocene bats with tropical affinities, the mormoopids *M. megalophylla* and *P. pristinus* are North American in origin, whereas the phyllostomids *D. archaeodaptes* and *D. stocki* and the molossids *E. floridanus* and *E. underwoodi* are South American (Morgan, 2005, 2008; Czaplewski et al., 2008). Peters' Ghost-faced Bat *M. megalophylla* has been identified from three Rancholabrean faunas in peninsular Florida, Rock Springs in central part of the state (Ray et al., 1963; Morgan, 1991) and Cutler Hammock and Monkey Jungle Hammock at the southern tip of the peninsula (Morgan, 2002). The modern distribution of *M. megalophylla* is from Texas south through Mexico to Honduras, with several disjunct populations in northern South America (Smith, 1972). The closest current records of *M. megalophylla* are from caves on the Edwards Plateau in southwestern Texas, about 1500 km west of peninsular Florida (Schmidly, 1991). However, there are locally extinct populations of *M. megalophylla* from Quaternary cave deposits on several islands in the West Indies that are much closer to Florida, including Cuba (Silva Taboada, 1974) and Abaco and Andros in the Bahamas (Morgan, 2001). It is not known if the Florida Pleistocene *M. megalophylla* was derived from the continental Neotropics or the West Indies.

Underwood's Mastiff Bat *E. underwoodi* is a large species in the family Molossidae known from a single Florida Rancholabrean site, Lecanto 2A (Morgan, 1991). *E. underwoodi* is a Neotropical species found from Central America north through Mexico to southernmost Arizona, no longer occurring within 2000 km of Florida (Hall, 1981). Another member of the genus *Eumops*, *E. floridanus*, is currently endemic to the southern third of the Florida peninsula (Koopman, 1971; Timm and Genoways, 2004), and also has been found in two late Pleistocene sites, Melbourne (Allen, 1932) and Monkey Jungle (Martin, 1977; Morgan, 1991). The extralimital *E. underwoodi* is readily separated from *E. floridanus* by its much larger size (Morgan, 1991).

There are three extinct bats from Florida Plio-Pleistocene faunas with Neotropical affinities, *P. pristinus*, *D. archaeodaptes*, and *D. stocki*. *P. pristinus*, in the endemic Neotropical family Mormoopidae, was identified from Monkey Jungle Hammock in southern Florida (Morgan, 1991). *P. pristinus* is known elsewhere only from Late Quaternary cave deposits in Cuba (Silva Taboada, 1974). Monkey Jungle is the only record of *Pteronotus* in the United States, fossil or recent. Species in this genus are otherwise restricted to the Neotropics in the West Indies and in Middle and South America (Smith, 1972).

Two extinct species of vampire bats in the genus *Desmodus* have been identified from late Pliocene and Pleistocene sites in Florida. The oldest fossil records of *Desmodus* are of *D. archaeodaptes* from the latest Blancan Inglis 1A LF and the early Irvingtonian Haile 16A and Haile 21A LFs (Morgan et al., 1988; Morgan, 1991). The larger Rancholabrean species *D. stocki* is known from four localities in Florida, Haile 1A, Haile 11B, Arredondo 2A, and Reddick 1, all of which are paleokarst deposits in the northern part of the state, as well as about ten late Pleistocene sites in West Virginia, the western United States, and Mexico (Ray et al., 1988; Grady et al., 2002). The family Phyllostomidae, including vampire bats, originated in South America; however, *Desmodus* is unknown on that continent prior to the late Pleistocene (Morgan et al., 1988; Ray et al., 1988). It has been hypothesized that *Desmodus* migrated northward from South America in the Pliocene following its primary food source, probably the blood of large slow-moving xenarthrans such as ground sloths and glyptodonts (Morgan, 1991). This hypothesis is supported by the earliest record of *Desmodus* from Inglis 1A, a late Pliocene site with a diverse fauna of large Interchange xenarthrans, including three cingulates and three ground sloths. McDonald and Jefferson (2008) noted a similarity in the late Pleistocene occurrences of *Desmodus* and the Shasta ground sloth *Nothrotheriops shastensis* in the western United States and northern Mexico, and suggested that *Nothrotheriops* may have been a favored source of blood for

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vampire bats. However, *D. stocki* also occurs in Rancholabrean sites in West Virginia and Florida where *Nothrotheriops* is absent, suggesting that vampires also fed on other ground sloths, such as *Megalonyx* and *Paramylodon*.

The extinct pocket gopher *O. propinetis* from several Florida late Blancan and early Irvingtonian faunas, including Inglis 1A and 1C and Haile 16A, appears to be tropical in origin (Martin, 1974a; Ruez, 2001). Although Wilkins (1984) originally referred *propinetis* to *Geomys*, Ruez (2001) transferred *G. propinetis* to the Neotropical genus *Orthogeomys* based on dental characters. Several genera in the North American family Geomyidae, including *Orthogeomys*, are now restricted to the Neotropics in Mexico and Central America. The living Hispid Pocket Gopher *O. hispidus* occurs as far north as southern Tamaulipas in northeastern Mexico (Hall, 1981).

There are five extralimital genera of small mammals with western affinities found in Florida during the Pliocene and Pleistocene, *Antrozous*, *Lepus*, *Spermophilus*, *Thomomys*, and *Baiomys*, none of which currently occurs within 1000 km of the Florida peninsula. The vespertilionid bat *Antrozous* sp. from the latest Blancan Inglis 1A LF (Morgan, 1991) is somewhat larger than the living Pallid Bat *A. pallidus*, a species restricted to western North America from British Columbia south to central Mexico and east to southern Texas (Hall, 1981). Two species in the jackrabbit genus *Lepus* occurred in Florida Plio-Pleistocene faunas, a medium-sized species tentatively referred to *L. townsendii* from the early Irvingtonian Leisey Shell Pit (Morgan and White, 1995) and a larger species approximately the size of *Lepus alleni* from Inglis 1A and the late Irvingtonian Coleman 2A (Martin, 1974a; Webb and Wilkins, 1984). The White-tailed Jackrabbit *L. townsendii* now occurs as far east as Missouri and Iowa, whereas the Antelope Jackrabbit *L. alleni* is a southwestern species found from southern Arizona south along the Pacific coast of Mexico to Nayarit (Hall, 1981). A ground squirrel of the genus *Spermophilus* similar to, and possibly conspecific with, the Thirteen-lined Ground Squirrel *S. tridecemlineatus*, has been identified from the Rancholabrean Haile 14A and Surprise Cave faunas in northern peninsular Florida (Martin, 1974b; this paper). *S. tridecemlineatus* occurs as far east as eastern Texas and Oklahoma (Hall, 1981). There are also extralimital records of *S. tridecemlineatus* from a number of Appalachian late Pleistocene cave deposits, from Pennsylvania and West Virgiana south to Tennessee, Georgia, and Alabama (McDonald, 2002). An extinct species of the smooth-toothed pocket gopher *Thomomys*, *T. orientalis*, occurs in the Irvingtonian Coleman 2A LF and the Rancholabrean Sabertooth Cave, Lecanto 2A, and Rock Springs LFs from Florida (Simpson, 1928; Wilkins, 1985; Morgan, 1991). The closest any living species of *Thomomys* occurs to Florida is Botta's Pocket Gopher *T. bottae* from southwestern Texas (Hall, 1981), about 2000 km west of the Florida peninsula. Ruez (2001) identified the pygmy mouse *Baiomys* from the latest Blancan Inglis 1C, a genus now represented by two species from the western United States, Mexico, and Central America. The only living species of *Baiomys* in the United States is *B. taylori*, found from Mexico north to eastern Texas, as well as southern Arizona and New Mexico (Hall, 1981).

The porcupine *Erethizon* is present in about ten Florida Blancan, Irvingtonian, and Rancholabrean sites (Frazier, 1981). There are two extinct species of late Blancan porcupines in Florida, *E. kleini* from Inglis 1A and *E. poyeri* from Haile 7C and Haile 7G; the extant *E. dorsatum* is known from at least five Florida Irvingtonian sites (Frazier, 1981; Hulbert, 1997; Hastings et al., 2006). *Erethizon* was a participant in the GABI and ultimately of South American origin. However, the living North American Porcupine *E. dorsatum* is now a temperate species and extralimital to Florida, occurring in coniferous forests in northern Michigan and New England south to Pennsylvania in the eastern U.S., but more widespread in western North America (Hall, 1981). The occurrence of *E. dorsatum* in several Florida Rancholabrean faunas, including the Aucilla River in the eastern panhandle and the Waccasassa River, New Port Richey, and Seminole Field along the Gulf Coast (Frazier, 1981; Morgan and White, 1995), probably represents an eastern extension of the western population of porcupines which now occurs no farther east than central Texas.

Two extralimital genera of rodents from Florida Pleistocene sites, *Zapus* and *Synaptomys*, currently occur well north of Florida. There is a single record of the jumping mouse *Zapus* from the early Irvingtonian Haile 16A LF (Morgan and Hulbert, 1995). The living Meadow Jumping Mouse *Zapus hudsonius* does not occur farther south than central Georgia and Alabama (Hall, 1981). The extinct bog lemming *Synaptomys australis* (considered a large subspecies of the living Southern Bog Lemming *S. cooperi* by some authors) was found in Rancholabrean faunas throughout the Florida peninsula as far south as the West Palm Beach LF (27° N) in Palm Beach County in the southern peninsula (Morgan, 2002). An earlier extinct species, *S. morgani*, was described from Haile 16A (Martin et al., 2003). *S. cooperi* now occurs no farther south than the Appalachians of North Carolina and Tennessee. Although the genus *Synaptomys* is restricted to northern latitudes at the present time, it appears that the large extinct species *S. australis* was adapted to warm temperate and subtropical climates. *S. australis* was one of the few small mammals in North America that went extinct in the late Pleistocene.

6. Discussion

Birds, mammals, and several species of reptiles with tropical or western affinities are found in Florida Pliocene and Pleistocene vertebrate faunas, several of which still inhabit the Florida peninsula. These distributional patterns indicate the presence of long-term, albeit intermittent, biogeographic corridors connecting Florida with both xeric habitats in western North America and tropical habitats in Middle America. These corridors appear to have been particularly active during glacial intervals when Florida experienced a drier climate with somewhat milder winters. The occurrence of both tropical and western taxa in some of the same faunas strongly indicates that these distributional patterns were integrally related and not mutually exclusive. Some of the same species of birds and mammals with extralimital Plio-Pleistocene records in Florida are currently found not only in tropical Mexico and Central America, but also northward along the southern Gulf Coast of Texas or in the arid Southwest from Texas to southern California. As a result, assignment of certain species as having western or tropical affinities is somewhat arbitrary (Table 1).

6.1. Effects of sea-level change

With the Atlantic Ocean on the east and the Gulf of Mexico on the west, the Florida peninsula was profoundly affected by sea-level changes associated with glacial and interglacial periods during the Ice Age. The most significant changes occurred during glacial intervals, such as the Wisconsinan glacial in the late Pleistocene when sea level was as much as 100 m lower than present and the Florida peninsula was more than twice its current land area (Emslie, 1998). During the Wisconsinan glacial maximum, the Florida Keys became joined to the southern tip of the peninsula and a large expanse of the shallow continental shelf in the Gulf of Mexico off the west coast of Florida would have been exposed as dry land. It has been hypothesized that during glacial intervals the exposed continental shelf along the northern margin of the Gulf of Mexico, from the west coast of Florida west to Louisiana and then south along the Texas coast to northern Mexico, supported savanna and thorn scrub habitats, the so-called "Gulf Coast savanna

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corridor" (Webb, 1974, 1978; Emslie, 1998). Another savanna corridor, or possibly a branch of the Gulf Coast savanna corridor, appears to have extended eastward, with connections from southern Arizona and northern Mexico east through Texas and along a southeastern corridor, enhancing the dispersal of western vertebrates into the Florida peninsula (Emslie, 1998). Although the Gulf Coast corridor is most often cited as having been comprised of arid grassland and scrub habitat, it is apparent from this study that this corridor must have been comprised of a mosaic of habitats including desert grassland, savanna, and oak/pine forests, all intermixed with wetlands. This habitat mosaic would have greatly facilitated the immigration of tropical forest, wetland, and savanna vertebrates into the Florida peninsula from Middle America, as well as arid land and wetland species from western North America (Emslie, 1998) as documented here.

To reach the Florida peninsula during the late Pliocene and Pleistocene, most tropical taxa probably migrated north along the Gulf of Mexico coastal plain from Mexico to Texas and then east to the Florida peninsula. However, it is possible that birds and bats may have flown from tropical Mexico across the Gulf of Mexico to the Florida peninsula during glacials when the distances were much reduced. During the late Wisconsinan low sea level stand, the Campeche Bank off the northern coast of the Yucatan peninsula and the southwesternmost extension of the Florida peninsula would have been as close as 400 km, compared to more than 800 km that now separate these two peninsulas. The majority of tropical vertebrates in southern peninsular Florida today are birds and bats of West Indian origin that appear to be recent (i.e., Holocene) immigrants, having flown across much narrower water gaps of about 150 km from either Cuba to the south or the Bahamas to the east.

Very few of the Neotropical species of mammals and birds known from Florida Plio-Pleistocene sites have been found in sites of similar age elsewhere on the Atlantic and Gulf coastal plains. Exceptions include *L. wiedii* (=*Felis amnicola*) from a few sites in Mississippi and Georgia (Werdelin, 1985), *P. onca* which was fairly widely distributed in Irvingtonian and Rancholabrean sites in the southeastern United States (Seymour, 1993), and *T. walleri* from the early Pliocene of the Texas Gulf Coastal Plain as well as three late Pliocene localities in Florida (MacFadden et al., 2007). This is more likely a result of a lack of suitable Plio-Pleistocene sites on the Gulf and Atlantic coastal plains from the Carolinas to Texas, than an absence of tropical species in this region. Outside of Florida, most Ice Age sites from the southeastern coastal plain consist of large mammals preserved in fluvial or deltaic depositional environments. The Florida peninsula has many paleokarst features such as caves, sinkholes, and fissures containing diverse samples of small terrestrial vertebrates of Plio-Pleistocene age (Morgan and Hulbert, 2008), including numerous examples of tropical and western birds and mammals (Table 1).

Most Pleistocene interglacials were characterized by sea levels near the current level or only slightly higher (5–10 m above modern level). However, there were several interglacial high sea level stands in the late Pliocene from 10 to 30 m above modern level (Krantz, 1991). The savanna corridors so prevalent during glacial periods appear to have been reduced or absent during interglacials because of the higher sea levels which, together with a reduction in habitat diversity, led to a rarity or absence of western and tropical species in most Florida interglacial vertebrate faunas (Emslie, 1998). The late Blancan Haile 15A LF from the north-central part of the peninsula occurs about 30 m above sea level (Robertson, 1976) and the late Blancan Kissimmee River and De Soto Shell Pit LFs from southern peninsular Florida are about 10 m above sea level (Morgan, 2005). All three of these sites contain diverse marine vertebrate faunas, confirming their deposition during interglacial high sea level stands. However, with the exception of large Interchange mammals such as glyptodonts, pampatheres, and ground sloths, these three late Blancan interglacial faunas generally lack species with western or tropical affinities (Morgan and Hulbert, 1995; Emslie, 1998; Morgan, 2005).

Emslie (1992, 1995, 1998) documented the extinction and consequent reduction in species richness of wetland birds in Florida during the Ice Age, especially in the late Pliocene and early Pleistocene, but also continuing until the end of the Pleistocene. He suggested that many of these extinctions occurred during interglacial high sea level stands, when much of the southern half of the Florida peninsula would have been underwater. With a sea level rise of 10 m, which occurred several times during the Pliocene, more than 50% of the Florida peninsula was submerged, whereas a sea level rise of 5 m, which occurred several times during the Pleistocene, would have flooded about a third of the peninsula. This loss of land area led to a reduction in habitat area which in turn resulted in a loss in diversity and the extinction/extirpation of many species of wetland birds (Emslie, 1998), as well as other species of birds and mammals. During glacial intervals, the area of the Florida peninsula was greatly increased, more than doubling the current land area during the maximum sea level drop of 100 m in the Wisconsinan. This greater land area was probably accompanied by an increase in habitat diversity, as well as the opening of dispersal corridors to western North America and tropical Middle America as discussed above. The species-area effect, commonly applied to island biogeography (e.g., MacArthur and Wilson, 1967; Morgan and Woods, 1986), predicts that larger islands (or a peninsula in the case of Florida) can support more species of birds and mammals (and other groups of animals and plants as well) than smaller islands because of their greater land area, which is generally associated with an increase in habitat diversity. The increase in species richness of birds and mammals in Florida during glacial intervals, in particular the appearance of western and tropical species, can be attributed to the greater area of the peninsula and presumed increase in habitat diversity, together with effective dispersal corridors to western North America and tropical Middle America. Moreover, these effects were probably even greater than currently understood, considering that many potential Ice Age sites are almost certainly submerged on the shallow continental shelf off the west coast of Florida in the Gulf of Mexico.

A specific example of the effect of sea level on vertebrate distributions in Florida involves the local extinction of several species of tropical cave-dwelling bats in the southern peninsula at the end of the Pleistocene. Two species in the Neotropical bat family Mormoopidae, the extralimital *M. megalophylla* and the extinct *P. pristinus*, occurred in Rancholabrean cave deposits in southern peninsular Florida, including *M. megalophylla* from Rock Springs and Cutler Hammock and both species from Monkey Jungle Hammock. All three sites would have consisted of fairly extensive dry cave systems in the late Pleistocene when sea level was as much as 100 m lower and water tables in the Florida peninsula were correspondingly lower as well. At the present time, Rock Springs is submerged and Cutler and Monkey Jungle are sediment-filled sinkholes just a few meters above sea level. Another cave-dwelling bat identified from these three sites, the Southeastern Myotis *Myotis austroriparius*, is also now absent from southern peninsular Florida. Because of the low topography and high water tables, there are currently no dry caves inhabited by bats in the southern half of the Florida peninsula (Morgan, 1991). Mormoopids typically are found in large caves in the continental Neotropics and the West Indies, generally preferring caves with a hot and humid microclimate, so-called hot caves (Morgan, 1999, 2001). Hot caves are now found in tropical regions, but apparently were present in the southernmost part of the Florida peninsula during the late

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Pleistocene low sea level stand. A similar pattern of extinction or extirpation among mormoopids and other obligate cave-dwelling bats has been documented for a number of islands in the West Indies, particularly small islands in the Bahamas, Cayman Islands, and Lesser Antilles, presumably for the same reason, the flooding of large cave systems by rising sea level and water tables during the latest Pleistocene and early Holocene (Morgan, 1999, 2001).

6.2. *Paleoclimatic implications*

Of particular interest to the discussion is the current northern extension of tropical forests and the eastern limits of extensive grasslands in North America, and possible changes in the distribution of these habitats during the late Pliocene and Pleistocene. Tropical forest habitats now reach northward to about 24° N latitude along the Gulf coastal lowlands in the state of Tamaulipas in northeastern Mexico, while subtropical thorn forest and thorn scrub habitats extend somewhat farther north into northern Tamaulipas and southern Texas. Koopman and Martin (1959) discussed the distribution of tropical mammals in northeastern Mexico, demonstrating that Neotropical species rapidly decrease from northern Veracruz and eastern San Luis Potosí north into southern Tamaulipas, between the latitudes of about 22° and 24° N, corresponding with the disappearance of tropical evergreen and tropical deciduous forests. Very few tropical mammals reach northern Tamaulipas or southern Texas, although quite a few Neotropical birds do occur in the Rio Grande valley of southernmost Texas.

There is little evidence for a widespread Ice Age expansion of the Neotropical flora and fauna into the southeastern United States. Only a limited number of tropical birds and mammals were able to extend their ranges eastward to the Florida peninsula during the Plio-Pleistocene, and most of those species occur in only one or several localities (Table 1). Among the extralimital tropical species found in Florida Plio-Pleistocene sites, many have broad ecological tolerances and occur widely throughout the New World tropics. For example, the three species of Neotropical cats found in Florida Pleistocene sites, *L. pardalis*, *L. wiedii*, and *P. onca*, now occur from southernmost Texas (*L. pardalis*, *P. onca*) or northern Mexico (*L. wiedii*) south through Central America to Brazil and Argentina. *L. wiedii* is an arboreal species found in dense forests, whereas *L. pardalis* and *P. onca* occur in a wider variety of tropical habitats, from rain forests to xeric scrub forests and savannas (Wilson and Ruff, 1999).

Although the appearance of tropical forms in Florida during glacial intervals seems counterintuitive, it actually makes sense when examined in closer detail. In addition to the lower sea levels and subsequent expansion of the Gulf Coast savanna corridor mentioned above, certain climatic factors during glacials also may have favored tropical birds and mammals in Florida. Much of temperate North America, including Florida, apparently had a more equable climate during glacial intervals (Pielou, 1991). Florida would have experienced a warm equable climatic regime during the Wisconsinan and earlier glacials, with somewhat milder winters and cooler summers compared to the warm continental climate found there today with its greater temperature extremes (Graham and Mead, 1987). The 10 °C minimum winter isotherm, representing the coolest temperatures that many tropical vertebrates can tolerate, now passes through the center of the Florida peninsula at about the latitude of Tampa at 28° N (McNab, 1973). Most of the tropical birds and bats found in Florida today occur in the southern half of the peninsula and the Keys, south of 28°. However, if winter temperatures were just a few degrees warmer during glacials, then the 10 °C winter isotherm would have moved northward several hundred km and the entire Florida peninsula would have been suitable for the survival of tropical species. Moreover, the Gulf Coast savanna corridor was almost certainly south of the 10 °C winter isotherm as well and the immigration of tropical species into Florida along the northern Gulf Coast would not have been limited by cool winter temperatures as it is today.

Several genera of Plio-Pleistocene vertebrates have been used previously to provide proxy data on climate or temperature regimes for sites in which they occur, in particular indicating the presence of warmer subtropical temperatures. Among the most prominent of these supposed climatic indicator taxa are the giant land tortoise *Hesperotestudo* (referred to *Geochelone* in much of the older literature) and the vampire bat *Desmodus*. *Hesperotestudo* has long been used as an indicator of a subtropical climate and frost-free winter conditions in North American Pliocene and Pleistocene faunas (Hibbard, 1960). Although widely distributed in southern North America until the Blancan and Irvingtonian, large species of *Hesperotestudo* became increasingly restricted in range during the Pleistocene. Large species of *Hesperotestudo* are unknown in the southwestern United States (New Mexico, Arizona, southern California) after the early Pleistocene (early Irvingtonian), probably as a result of cooling temperatures and increasing aridity (Thompson, 1991; Morgan et al., 2008). A much smaller species, *H. wilsoni*, is known from several southwestern late Pleistocene cave deposits (Harris, 1993).

The large land tortoise *H. crassiscutata* is primarily restricted to Florida and the southeastern United States during the Rancholabrean, with records from South Carolina west to the Texas Gulf coastal plain (Auffenberg, 1974). The living species of giant land tortoises, such as the Galapagos tortoise *Chelonoidis nigra* (also formerly referred to *Geochelone*), are restricted to the tropics. They are too large to construct burrows to escape cold temperatures, and thus are extremely susceptible to freezing conditions. Cassiliano (1997) reviewed the physiology, ecology, and distribution of the living species of giant land tortoises. His conclusions about the temperature-controlled geographic distribution of living giant land tortoises supported Hibbard's (1960) original hypothesis that the presence of *Hesperotestudo* (=*Geochelone*) in a fossil site does appear to indicate a subtropical to tropical climate and the absence of freezing temperatures. Fossils of large *Hesperotestudo* occur in many Florida Plio-Pleistocene faunas, including the majority of the sites discussed that contain extralimital species of tropical birds and mammals. The distribution of giant land tortoises suggests that most of the Florida peninsula was south of the 10 °C minimum winter isotherm and had a subtropical climate during the Pliocene and Pleistocene, including during the Wisconsinan glacial as indicated by the presence of *H. crassiscutata* is many Florida late Rancholabrean sites (Auffenberg, 1974). The northern half of the Florida peninsula is currently north of the 10 °C minimum winter isotherm and experiences occasional periods of freezing temperatures up to several days in duration during the winter months.

Desmodus is the only genus of bat in the primarily Neotropical bat family Phyllostomidae that made a significant incursion into temperate North America during the late Pliocene and Pleistocene (Ray et al., 1988; Morgan, 1991). The extant Common Vampire Bat *Desmodus rotundus* occurs throughout tropical America, from South America and Central America north to Tamaulipas in northeastern Mexico and Sonora in northwestern Mexico (Hall, 1981). At the present time, the 10 °C minimum winter isotherm passes through southern Tamaulipas at about the Tropic of Cancer (~23° N), marking the northernmost occurrence of many tropical species, including *D. rotundus* (McNab, 1973). However, it seems highly unlikely that the 10 °C winter isotherm extended as far north as Potter Creek Cave in northern California (40°47′N) or New Trout Cave, West Virginia (38°36′N), the two northernmost late Pleistocene records of the extinct vampire *D. stocki* (Hutchison, 1967; Grady et al., 2002), especially since these two faunas do not record

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the presence of any other tropical vertebrates. The larger body size and more northerly distribution of *D. stocki* suggest this species was able to tolerate somewhat cooler winter temperatures than living vampire bats. Moreover, records of *D. stocki* from temperate North America are restricted to the late Pleistocene (Wisconsinan) glacial interval that was characterized by more equable climatic conditions than at present, particularly milder winters. Living vampire bats are nonmigratory nor do they hibernate, thus it is unlikely that *D. stocki* migrated south or hibernated during the winter months. The extinct species *D. archaeodaptes*, similar in size to extant *D. rotundus*, is known from three Florida latest Pliocene and early Pleistocene sites that presumably were south of the 10 °C minimum winter isotherm at that time. However, large size among vampire bats is not necessarily correlated with greater tolerance for cooler temperatures, as the largest known vampire bat, the extinct species *D. draculae*, is known only from late Pleistocene sites in the New World tropics, from the Yucatan peninsula in southern Mexico (Arroyo-Cabrales and Ray, 1997) and Belize (Czaplewski et al., 2003) south to Venezuela (Morgan et al., 1988) and Brazil (Czaplewski and Cartelle, 1998).

Extensive grasslands typical of the Great Plains and xeric grasslands found in the southwestern deserts, and most species of mammals and birds adapted to these grasslands habitats, now occur no farther east than Texas. The most prominent grasslands-adapted taxa in Florida Plio-Pleistocene sites that are now extralimital to the state are the jackrabbit *Lepus*, ground squirrel *Spermophilus*, pocket gopher *Thomomys*, and the Greater Prairie Chicken *T. cupido*. *Spermophilus*, *Thomomys*, and *T. cupido* also occur in Pleistocene sites in the Appalachians (Kurtén and Anderson, 1980; McDonald, 2002), suggesting that the eastward expansion of grasslands during glacials was fairly widespread in eastern North America, from Pennsylvania and West Virginia south to Florida. Another bird typical of western grasslands, the Burrowing Owl *A. cunicularia*, occurs in several Florida Plio-Pleistocene sites and still survives in the state but not elsewhere in eastern North America. Other extralimital taxa with western affinities in Florida sites are found in a wider variety of habitats in western North America, including the pallid bat *Antrozous*, pygmy mouse *Baiomys*, California Condor *G. californianus*, Golden Eagle *A. chrysaetos*, Band-tailed Pigeon *C. fasciata*, and Black-billed Magpie *P. pica*.

Florida would appear to be situated in an ideal geographic location to record the presence of north temperate or even boreal vertebrates that extended their ranges farther south during glacial periods in the Pleistocene. However, such is not the case. Despite Colbert's (1942) characterization of Florida as an "Ice Age winter resort," the Florida Plio-Pleistocene record documents very few species of mammals or birds now restricted to north temperate or boreal latitudes that migrated farther south. The only extralimital or extinct northern species in Florida Pleistocene faunas are the Ruffed Grouse *B. umbellus*, the Saw-whet Owl *A. acadicus*, the extinct chipmunk *T. aristus*, the jumping mouse *Zapus*, and the extinct bog lemmings *S. australis* and *S. morgani*. Presumably, the subtropical to warm temperate climate of the Florida peninsula was (and still is) unsuitable for the survival of most northern species. Boreal/arctic mammals occur in late Pleistocene glacial faunas in eastern North America as far south as about 35° N (northern Arkansas east to the Appalachians in eastern Tennessee, northern Alabama and northern Georgia), but are not known farther south on the Gulf or Atlantic coastal plains, including Florida. Much like today, the absence of boreal mammals from warm temperate to subtropical latitudes during glacials is probably associated with physiological and ecological factors relating to warm summer temperatures. Although few in number, there are several examples of subtropical mammals occurring farther north in Midwestern and Appalachian sites during the Rancholabrean, including the large extinct armadillo *D. bellus* from sites as far north as West Virginia, Indiana, Missouri, and Iowa (Klippel and Parmalee, 1984) and the extinct tapir *T. veroensis* from Pennsylvania, West Virginia, and Kentucky (Graham, 2003). These northern occurrences of armadillos and tapirs are most common during the Wisconsinan, further supporting the hypothesis of milder winter conditions during glacials.

7. Conclusion

This review of Ice Age vertebrate faunas in Florida provides a new perspective on nonanalog communities in this unique region of North America and on climatic factors that shaped both fossil and modern communities over the past 2.5 Ma. There is no doubt that each glacial cycle varied in how it impacted local temperatures and subsequent responses by plants and animals. However, the general patterns that occurred do show some consistent trends in how habitat corridors opened and closed over millennia, allowing tropical and western taxa access to the Florida peninsula during glacial intervals. The fate of those taxa during interglacials is varied, with many going extinct while others survived. The disjunct distribution of birds and mammals (as well as some plants and reptiles) that are found in Florida today is a testament to this long period of climate change during the Ice Age. The authors look forward to future additions to the Florida fossil record that will continue to modify and test the concepts presented here.

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