OVERVIEW OF THE GEOLOGY AND VERTEBRATE BIOCHRONOLOGY OF THE LEISEY SHELL PIT LOCAL FAUNA, HILLSBOROUGH COUNTY, FLORIDA

Gary S. Morgan[1] and Richard C. Hulbert, Jr.[2]

ABSTRACT

The Leisey Shell Pit Local Fauna was collected from two adjacent commercial shell mines located 7 km southwest of Ruskin and less than 1 km inland from Tampa Bay in Hillsborough County, Florida. Leisey Shell Pit is one of the most diverse Irvingtonian vertebrate faunas in North America, composed of at least 203 species: 14 sharks, 9 rays, 50 bony fish, 3 amphibians, 26 reptiles, 52 birds, and 49 mammals. Leisey 1A and Leisey 3A are the largest of the four principal sites that constitute the Leisey Shell Pit Local Fauna. Leisey 1A has extensive samples of large mammals, in particular: the camelids *Palaeolama mirifica* and *Hemiauchenia macrocephala*, two species of *Equus*, the primitive mammoth *Mammuthus hayi*, the ground sloths *Paramylodon harlani* and *Nothrotheriops texanus*, the giant tapir *Tapirus haysii*, the peccary *Platygonus vetus*, the gracile sabercat *Smilodon gracilis*, the short-faced bear *Arctodus pristinus*, and the canid *Canis edwardii*. The large mammal fauna from Leisey 3A is dominated by associated juvenile skeletons of *Hemiauchenia macrocephala*, while its diverse microvertebrate assemblage contains important samples of freshwater fish, sirens, aquatic snakes, birds, and small mammals.

Sediments in the Leisey Shell Pit are referred to four formations, each of which has produced vertebrate fossils. At the base of the stratigraphic section is an indurated, tan to light gray dolostone referred to the Arcadia Formation. A horse tooth identified as "*Merychippus*" *tertius* derived from this unit is indicative of an early Barstovian age (early middle Miocene). Reworked sediments on top of the Arcadia Formation contain several land mammals, including the horses *Nannippus aztecus*, *Neohipparion eurystyle*, and *Cormohipparion ingenuum*, whose association is characteristic of Florida late early Hemphillian (late Miocene) faunas. Phosphatic gravel and spheroidal metaquartzite pebbles in this unit are typical of the upper Bone Valley Formation. The major concentrations of vertebrate fossils in the Leisey Shell Pit occur in thin, irregular layers of organic-rich sediment distributed throughout about 7 m of sandy marine shell beds referred to the Bermont Formation, which unconformably overlies the Arcadia Formation. The large assemblage of land mammals from these organic units in the Bermont Formation is early Irvingtonian (early Pleistocene) in age. Shell beds of the Fort Thompson Formation occur in the Leisey section above an

[1] The senior author is a paleontologist at the New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque NM 87104-1375 (formerly a Senior Biological Scientist at the Florida Museum of Natural History, P.O. Box 117800, Gainesville FL 32611-7800, USA).

[2] The junior author is an Assistant Professor of Geology at Georgia Southern University, Statesboro GA 31460-8149, USA.

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erosional unconformity at the top of the Bermont Formation. The Fort Thompson shell beds contain a distinctly younger mammalian fauna, including the bison *Bison* sp., the cotton rat *Sigmodon hispidus*, and the tapir *Tapirus veroensis*, typical of the late Pleistocene (Rancholabrean).

Geochronological data derived from paleomagnetic analysis, strontium isotope geochronology, sea levels, and molluscan and vertebrate biochronology have been incorporated in a multidisciplinary effort to determine the age of the Bermont Formation at the Leisey Shell Pit. Molluscan biochronology implies an early or middle Pleistocene age, whereas mammalian biochronology is considerably more precise strongly favoring an early Pleistocene age between 1.6 and 1.0 Ma. All paleomagnetic samples from the Bermont Formation at Leisey have reversed polarity and are referred to the Matuyama Chron, indicating an age greater than 0.78 Ma. The Leisey Bermont section does not correlate to the Jaramillo Subchron of normal polarity between 1.07 and 0.99 Ma. It is also unlikely the Leisey beds were deposited during the youngest portion of the Matuyama between 0.99 and 0.78 Ma. The combination of data from magnetic polarity, mammalian biochronology, and sea level strongly indicates that the Bermont Formation at Leisey is older than 1.07 Ma and younger than 1.55 Ma. Strontium isotope ratios from *Chione cancellata* (Mollusca) shells from Leisey indicate an age between 1 and 2 Ma.

Leisey is younger than Florida's best known earliest Irvingtonian (latest Pliocene) faunas, Inglis 1A and De Soto Shell Pit, based on the presence of five genera unknown in North America before the Pleistocene: *Nothrotheriops*, *Lutra*, *Castoroides*, *Palaeolama*, and *Mammuthus*. Four rodents from Leisey, *Geomys pinetis*, *Erethizon dorsatum*, *Sigmodon libitinus*, and *Ondatra annectens*, differ at the species level from their congeners at Inglis and De Soto. Leisey also lacks various Blancan holdover species found in the two older faunas, including the dwarf Florida form of *Megalonyx leptostomus*, *Chasmaporthetes ossifragus*, *Trigonictis macrodon*, and *Capromeryx arizonensis*. The occurrence of numerous species at Leisey that are unknown after the early Irvingtonian, including *Glyptotherium arizonae*, *Pachyarmatherium leiseyi*, *Holmesina floridanus*, *Nothrotheriops texanus*, *Sigmodon libitinus*, and *Canis edwardii*, further constrains the age of this fauna, ruling out a middle Irvingtonian or younger age assignment. The Leisey mammalian fauna correlates most closely with the late early Irvingtonian, between about 1.6 and 1.0 Ma. Other Florida faunas similar in age to Leisey are Haile 16A, Haile 21A, Crystal River Power Plant, Pool Branch, Payne Creek Mine, Rigby Shell Pit, and Punta Gorda. Of these sites Haile 16A is probably somewhat older (between 1.6 and 1.3 Ma) based on the occurrence of several holdovers from Florida late Blancan and earliest Irvingtonian faunas, including *Sylvilagus webbi*, *Geomys propinetis*, and *Trigonictis*.

Western early Irvingtonian faunas that are correlatives of Leisey include: Gilliland, Texas; Holloman, Oklahoma; Kentuck, Nash, and Wathena in Kansas; Sappa, Nebraska; and Java, South Dakota. Among these sites, Leisey has the largest number of diagnostic taxa in common with the Gilliland Local Fauna, including *Glyptotherium arizonae*, a medium-sized *Holmesina floridanus*, *Nothrotheriops texanus*, *Canis edwardii*, *Tapirus haysii*, and primitive *Mammuthus*. Leisey and other late early Irvingtonian faunas are younger than earliest Irvingtonian faunas (2.0 to 1.6 Ma) such as Curtis Ranch, Arizona and Inglis 1A and De Soto Shell Pit of Florida, and are older than middle Irvingtonian faunas (1.0-0.6 Ma), including: the type Irvington fauna from California; Cudahy, Kansas; Conard Fissure, Arkansas; Cumberland Cave, Maryland; Port Kennedy Cave, Pennsylvania; Hamilton Cave, West Virginia; and the Florida equivalent McLeod Limerock Mine.

The occurrence of land mammals in estuarine, freshwater, and terrestrial units within the predominantly nearshore marine late Pliocene and Pleistocene shell bed sequence of southern peninsular Florida (Pinecrest Beds, Caloosahatchee Formation, Bermont Formation, and Fort Thompson Formation in ascending stratigraphic order) has allowed a precision in dating these deposits not previously possible. The Pinecrest Beds, the uppermost unit of the Tamiami Formation, contain land mammal faunas of late Blancan age (2.5-2.0 Ma) based on the association of *Nannippus* and a large suite of Neotropical immigrants, including *Dasypus*, *Holmesina*, *Glyptotherium*, *Glossotherium*, *Eremotherium*, and *Neochoerus*. Florida late Blancan faunas derived from the Pinecrest Beds, or found in association with Pinecrest molluscan faunas, include Macasphalt Shell Pit, Acline Shell Pit, St. Petersburg Times, Kissimmee River, Brighton Canal, and Lehigh Acres. Vertebrate faunas from the overlying Caloosahatchee Formation lack typical Blancan forms, including *Borophagus*, *Nannippus*, *Equus* (*Dolichohippus*), and *Rhynchotherium*, and contain taxa typical of earliest Irvingtonian (2.0-1.6 Ma) faunas, such as Inglis 1A. The two richest earliest

Irvingtonian faunas from the Caloosahatchee Formation in southern Florida are the De Soto Shell Pit and Forsberg Shell Pit. Vertebrate faunas from the Bermont Formation are late early Irvingtonian (1.6-1.0 Ma) in age, and are typified by the Leisey Shell Pit, as well as Rigby Shell Pit, Crystal River Power Plant, and Punta Gorda. Vertebrate faunas associated with the Fort Thompson Formation typically contain *Bison* and other taxa characteristic of the Rancholabrean Land Mammal Age.

RESUMEN

La Fauna Local del Depósito de Conchuelas de Leisey fue colectada de dos minas de conchuela comerciales adyacentes y localizadas 7 km al suroeste de Ruskin y a menos de 1 km tierra adentro de la Bahía de Tampa, en el Condado Hillsborough, Florida. La fauna de vertebrados del Depósito de Conchuelas de Leisey es una de las más diversas del Irvingtoniano en Norte América, estando compuesta de por lo menos 203 especies: 14 tiburones, 9 rayas, 50 peces teleósteos, 3 anfibios, 26 reptiles, 52 aves y 49 mamíferos. Leisey 1A y Leisey 3A son los mayores de cuatro sitios principales que constituyen la Fauna Local de los Depósitos de Conchuelas de Leisey. Leisey 1A contiene vastas muestras de grandes mamíferos, en particular: los camélidos *Palaeolama mirifica* y *Hemiauchenia macrocephala*; dos especies de *Equus*; el mamut primitivo *Mammuthus hayi*; los perezosos terrestres *Paramylodon harlani* y *Nothrotheriops texanus*; el tapir gigante *Tapirus haysii*; el pecarí *Platygonus vetus*; el tigre dientes de sable grácil *Smilodon gracilis*; el oso de rostro corto *Arctodus pristinus*; y el cánido *Canis edwardii*. La fauna de grandes mamíferos de Leisey 3A es dominada por esqueletos asociados de juveniles de *Hemiauchenia macrocephala*, mientras que su diverso ensamblaje de microvertebrados contiene muestras importantes de peces de agua dulce, salamandras, culebras acuáticas, aves y pequeños mamíferos.

Los sedimentos en el Depósito de Conchuelas de Leisey son referidos a cuatro formaciones, cada una de las cuales ha producido fósiles de vertebrados. En la base de la sección estratigráfica se encuentra una dolostona endurecida marrón a gris claro, referida como Formación Arcadia. Un diente del caballo identificado como "*Merychippus*" *tertius* derivado de esta unidad es indicativo de una edad del Barstoviano temprano (principios del Mioceno medio). Los sedimentos retrabajados encontrados encima de la Formación Arcad ia contienen varios mamíferos terrestres, incluyendo los caballos *Nannippus aztecus*, *Neohipparion eurystyle* y *Cormohipparion ingenuum* cuya asociación es característica de las faunas de fines del Hemphilliano temprano de Florida (Mioceno tardío). Las gravas fosfáticas y piedrecillas esferoidales de metaquarzita en esta unidad son típicas de la Formación superior del Valle Hueso. Las mayores concentraciones de vertebrados fósiles en el Depósito de Conchuelas de Leisey ocurren en delgadas e irregulares capas de sedimentos ricos en materia orgánica distribuidos a lo largo de aproximadamente 7 m de camas arenosas de conchuelas marinas referidas como a la Formación Bermont, la cual se ubica sobre la Formación Arcadia. El vasto ensamblaje de mamíferos terrestres encontrados en estas unidades orgánicas en la Formación Bermont pertenece al Irvingtoniano temprano (Pleistoceno temprano). Camas de conchuelas pertenecientes a la Formación Fort Thompson ocurren en la sección Leisey por sobre una inconformidad erosiva encima de la Formación Bermont. Las camas de conchuelas de Fort Thompson contienen una fauna de mamíferos distintivamente más jóven, e incluyen a: el bisón *Bison* sp., la rata de algodón *Sigmodon hispidus* y el tapir *Tapirus veroensis*, todos típicos del Pleistoceno tardío (Rancholabreano).

En un esfuerzo multidisciplinario para determinar la edad de la Formación de Bermont en el Depósito de Conchuelas de Leisey, se han incorporado datos geocronológicos derivados de análisis paleomagnéticos; geocronología de isótopos de estroncio; niveles del mar y biocronología de moluscos y vertebrados. La biocronología de moluscos indica una edad del Pleistoceno temprano o medio, mientras que la biocronología de mamíferos es considerablemente más precisa, favoreciendo fuertemente una edad del Pleistoceno temprano, de entre 1.6 y 1.0 Ma. Todas las muestras paleomagnéticas de la Formación Bermont en Leisey tienen una polaridad revertida y son referidas al Cron de Matuyama, indicando una edad mayor que 0.78 Ma. La sección de Bermont en Leisey no se correlaciona con el Subcron de Jaramillo de polaridad normal, de entre 1.07 y 0.99 Ma. Es también poco probable que las camas de Leisey hayan sido depositadas durante la porción más jóven de Matuyama, entre 0.99 y 0.78 Ma. La combinación de datos de polaridad magnética, biocronología de mamíferos y niveles del mar indican fuertemente que la Formación Bermont en Leisey es más antigua que 1.07 Ma y más reciente que 1.55 Ma. La proporción de isótopos de estroncio

obtenidos de conchas de *Chione cancellata* (Mollusca) de Leisey indica una edad de entre 1 y 2 Ma.

En base a la presencia de cinco géneros desconocidos en Norte América antes del Pleistoceno (*Nothrotheriops, Lutra, Castoroides, Palaeolama* y *Mammuthus*), la fauna de Leisey es más jóven que otras faunas mejor conocidas del Irvingtoniano más temprano de Florida (Plioceno más tardío): Inglis 1A y el Depósito de Conchuelas de De Soto. Cuatro roedores de Leisey difieren a nivel de especie de sus congéneres de Inglis y De Soto: *Geomys pinetis, Erethizon dorsatum, Sigmodon libitinus* y *Ondatra annectens*. Leisey también carece de varios sobrevivientes del Blancano, los cuales se encuentran en las otras dos faunas más antiguas: la forma enana de Florida de *Megalonyx leptostomus, Chasmaporthetes ossifragus, Trigonictis macrodon* y *Capromeryx arizonensis*. La presencia de numerosas especies en Leisey desconocidas para después del Irvingtoniano temprano, tales como *Glyptotherium arizonae, Pachyarmatherium leiseyi, Holmesina floridanus, Nothrotheriops texanus, Sigmodon libitinus* y *Canis edwardii*, constriñen aún más la edad de esta fauna, descartando una edad del Irvingtoniano medio o más reciente. La fauna de mamíferos de Leisey se correlaciona más cercanamente con fines del Irvingtoniano temprano, entre aproximadamente 1.6 y 1.0 Ma. Otras faunas de Florida de similar edad a Leisey son: Haile 16A, Haile 21A, Planta Eléctrica de Crystal River, Pool Branch, Mina Payne Creek, Depósito de Conchuelas de Rigby y Punta Gorda. De estos sitios, Haile 16A es probablemente algo más antiguo (entre 1.6 y 1.3 Ma) en base a la ocurrencia de varios sobrevivientes de las faunas del Blancano tardío y el más temprano Irvingtoniano de Florida, tales como *Sylvilagus webbi, Geomys propinetis* y *Trigonictis*.

Entre las faunas Irvingtonianas del oeste que son correlativas a Leisey se incluyen a: Gilliland, Texas; Holloman, Oklahoma; Kentuck, Nash y Wathena en Kansas; Sappa, Nebraska; y Java, Dakota del Sur. De entre estos sitios, Leisey comparte un número mayor taxas de diagnósticas con la Fauna Local de Gilliland, incluyendo *Glyptotherium arizonae*, una *Holmesina floridanus* de tamaño medio, *Nothrotheriops texanus, Canis edwardii, Tapirus haysii* y un *Mammuthus* primitivo. Leisey y otras faunas del Irvingtoniano temprano son: más jóvenes que faunas del Irvingtoniano más temprano (2.0 a 1.6 Ma), tales como Rancho Curtis, Arizona e Inglis 1A y el Depósito de Conchuelas de De Soto en Florida; y: más antiguas que faunas del Irvingtoniano medio (1.0-0.6 Ma), incluyendo la Formación tipo de Irvington en California; Cudahy, Kansas; Fisura Conard, Arkansas; Cueva Cumberland, Maryland; Cueva Puerto Kennedy, Pennsylvania; Cueva Hamilton, Virginia del Oeste; y el equivalente de Florida, la mina McLeod Limerock.

La ocurrencia de mamíferos terrestres en unidades estuarinas, de agua dulce y terrestres dentro de la sequencia de camas de conchuelas predominantemente marinas y costeras de el sur de Florida peninsular pertenecientes al Plioceno tardío y al Pleistoceno (Camas de Pinecrest, Formación Caloosahatchee, Formación Bermont y Formación Fort Thompson, en orden estratigráfico ascendente) ha permitido una precisión en la determinación de su edad previamente imposible. Las Camas de Pinecrest, que constituyen la unidad más superior de la Formación Tamiami, contienen faunas de mamíferos terrestres del Blancano tardío (2.5-2.0 Ma), en base a la asociación de *Nannippus* y una gran variedad de inmigrantes Neotropicales, que incluyen *Dasypus, Holmesina, Glyptotherium, Glossotherium, Eremotherium* y *Neochoerus*. Las faunas del Blancano tardío de Florida derivadas de las Camas de Pinecrest, o encontradas en asociación con faunas de moluscos de Pinecrest incluyen el Depósito de Conchuelas de Macasphalt, el Depósito de Conchuelas de Acline, St. Petesburg Times, Río Kissimmee, Canal Brighton y Lehigh Acres. Las faunas de vertebrados de la Formación sobrepuesta de Caloosahatchee carecen de formas Blancanas típicas, incluyendo *Borophagus, Nannippus, Equus* (*Dolichohippus*) y *Rhynchotherium*, e incluyen taxas típicas del Irvingtoniano más temprano (2.0-1.6 Ma), tales como Inglis 1A. Las faunas más ricas del Irvingtoniano más temprano de la Formación Caloosahatchee en el sur de Florida son el Depósito de Conchuelas de De Soto y el Depósito de Conchuelas de Forsberg. Las faunas de vertebrados de la Formación Bermont son de fines del Irvingtoniano temprano (1.6-1.0 Ma) y son tipificadas por el Depósito de Conchuelas de Leisey, así como también el Depósito de Conchuelas de Rigby, la Planta Eléctrica de Crystal River y Punta Gorda. Las faunas de vertebrados asociadas con la Formación Fort Thompson contienen típicamente *Bison* y otras taxas características de la Edad de Mamíferos Terrestres del Rancholabreano.

INTRODUCTION

A remarkable concentration of early Pleistocene (Irvingtonian) vertebrate fossils was discovered by Frank Garcia in July 1983 after it was uncovered by a dragline during routine mining operations at the Leisey Shell Pit. This rich bone bed, designated Leisey Shell Pit 1A, is located about 7 km southwest of Ruskin in Hillsborough County, Florida (27°42'N latitude, 82°30'W longitude). Field teams from the Florida State Museum (now the Florida Museum of Natural History) and a large volunteer crew organized by the Tampa Bay Mineral and Science Club excavated the Leisey Shell Pit 1A Site almost continuously from April to September 1984. The total areal extent of the bone bed was approximately 2000 m^2, about 1300 m^2 of which was excavated during 1984, whereas 700 m^2 had been dug by avocational paleontologists in 1983. All fossils recovered in 1984 are housed in the Vertebrate Paleontology Collection of the Florida Museum of Natural History, University of Florida (UF).

Frank Garcia discovered a second rich concentration of vertebrate fossils at Leisey in November 1986, this time in a newly opened pit on the north side of Gulf City Road, only about 0.5 km north of Leisey 1A (Fig. 1). This site, Leisey Shell Pit 3A, was dug by Garcia and a volunteer field crew, as well as UF personnel, between November 1986 and February 1987. Although not as rich as Leisey 1A in numbers of species or individuals of large mammals, Leisey 3A in many ways complements the fauna from the original site, particularly in the comparatively large samples of freshwater and terrestrial microvertebrates. The most characteristic aspect of the Leisey 3A site is the abundance of the long-limbed llama, *Hemiauchenia macrocephala*, especially juvenile individuals.

The Leisey Shell Pit Local Fauna (LF), named by Hulbert and Morgan (1989), is composed of vertebrate fossils collected from Leisey Shell Pit 1A and 3A, as well as two other smaller sites, Leisey Shell Pit 1B and 3B. The four named Leisey sites are located in two nearly contiguous shell pits mined by the Leisey Shell Corporation. These concentrations of vertebrate fossils occur in thin layers or lenses throughout a stratigraphic interval of about 7 m within the predominantly marine shell beds of the Bermont Formation. The two shell pits, along with a third pit owned by the same corporation, have been assigned numbers (Leisey Shell Pit 1-3) and each major concentration of bones within a numbered pit has been given a letter designation. This is the standard system now used by the UF vertebrate paleontology program for naming and numbering specific localities within commercial quarrying operations. For example, Leisey Shell Pit 1A (shortened to Leisey 1A for convenience) specifies only those fossils recovered from the large site collected in 1983-1984. Fossils not from designated sites, often those collected

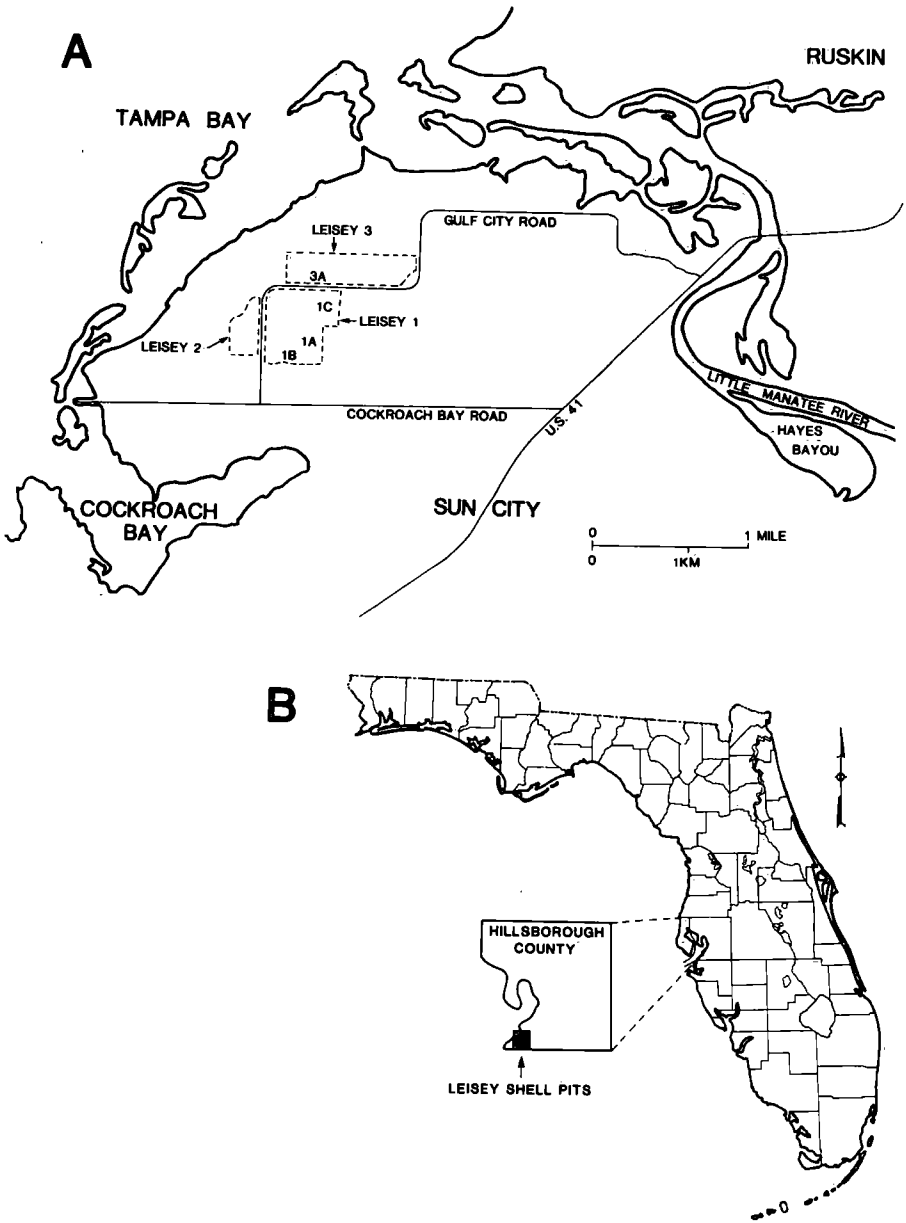

Figure 1. (A) Map of the Leisey Shell Pit region showing the location of the three Leisey pits and the four vertebrate-bearing sites mentioned in the text. (B) Map showing general location of the Leisey Shell Pit in Florida and Hillsborough County.

from excavation spoil piles, are assigned a quarry number, but not a letter (e.g. Leisey Shell Pit 2). This supercedes a previous system that used roman numerals to designate quarry numbers (e.g. Coleman IIA is now Coleman 2A).

The maps in Figure 1 show the location of the three Leisey Shell Pits in southwestern Hillsborough County. Leisey 1 is located in the SW¼ of section 15 and Leisey 3 is in the S½ of the NW¼ and the S½ of the NE¼ of section 15, T32S, R18E, Ruskin Quadrangle (USGS 7.5 minute series, 1981). Leisey 2 is in the SE¼ of section 16, T32S, R18E, Cockroach Bay Quadrangle (1969). The exact coordinates of the two Leisey sites that have produced the vast majority of the vertebrate fossils upon which the papers in this volume are based are as follows: Leisey Shell Pit 1A (NW¼, SE¼, SW¼ Sec. 15, T32S, R18E) and Leisey Shell Pit 3A (SW¼, SE¼, NW¼ Sec. 15, T32S, R18E). Leisey 1A and 3A were completely excavated in 1983-1984 and 1986-1987, respectively, and have since been destroyed by mining operations. Although Leisey 1A and 3A are the largest and richest sites in the Leisey Shell Pit, there are numerous other Leisey sites, three of which have been given separate designations (Leisey 1B, 1C, and 3B; see Fig. 1).

Because all three Leisey pits are less than 1 km inland from Tampa Bay to the west and are below 3 m in elevation, the local water table in this region is very near the ground surface. Most of the important bone concentrations were actually below mean sea level (i.e. more than 3 m below the present ground surface). Like most other commercial shell mining operations along Florida's Gulf Coast, the water levels in the Leisey pits are maintained at artifically low levels by pumping so that mining can be conducted above water. The Leisey 1 and 2 pits are no longer being actively mined and have been allowed to fill with water. Mining ceased at Leisey 3 in 1992 and it will subsequently flood as well.

There are no in-place samples of vertebrate fossils from Leisey 2 in the UF collection. Leisey 2 is also the only one of the three pits that contains a substantial number of Rancholabrean fossils, although Irvingtonian vertebrates are common in this pit as well. We have been unable to confidently establish the age of many of the specimens from Leisey 2 because they were collected from spoil piles, and thus have excluded them from this analysis and from the Leisey Shell Pit LF.

The Leisey Shell Pit LF is one of the richest early Pleistocene (Irvingtonian) vertebrate faunas in North America, both in terms of numbers of species and individuals. The vertebrate assemblage from Leisey is composed of 203 species, including 23 species of cartilaginous fish (14 sharks and 9 rays), 50 species of bony fish, 3 amphibians, 26 reptiles, 52 birds, and 49 mammals. Table 1 provides a complete vertebrate faunal list for the Leisey Shell Pit LF. To date, over 15,000 specimens of vertebrate fossils have been catalogued from the Leisey Shell Pit LF, the majority of which are from Leisey 1A. Most of the mammal papers in this volume are based primarily on material from Leisey 1A. However, Leisey 3A has a much richer vertebrate microfauna than does Leisey 1A, and consequently the

papers on fish, amphibians and reptiles, birds, and small mammals contain considerable data on fossils from Leisey 3A.

ACKNOWLEDGMENTS

This review represents a compilation of data from a variety of sources, including field studies at Leisey and other Florida Pliocene and Pleistocene sites by ourselves and many others, study of the extensive collections of Plio-Pleistocene vertebrate fossils housed in the Florida Museum of Natural History, and a comprehensive review of the literature on this topic. We thank the many contributors to this volume who permitted us to briefly summarize their work so that we could provide a complete vertebrate faunal list and a reasonably comprehensive review of the geochronology and biochronology of the Leisey Shell Pit. We are especially grateful to the authors of the papers on the various vertebrate groups who allowed us to combine the individual faunal lists from their papers in order to produce a complete vertebrate faunal list for the Leisey Shell Pit Local Fauna (Table 1).

As with all of the contributors to this volume, we are very grateful to the personnel of the Leisey Shell Corporation for all of their support and to the hundreds of volunteers who worked with the Florida Museum of Natural History in the excavation of the Leisey Shell Pit Sites 1A and 3A. The Preface to this volume should be consulted for more extended acknowledgments regarding the assistance provided by the Leisey Shell Corporation and the dedicated volunteer crews co-ordinated by the Tampa Bay Fossil Club. We would also like to thank several of our colleagues, including Steven D. Emslie, David Kendrick, Arthur R. Poyer, and Ann E. Pratt, who over the past ten years have participated "above and beyond the call of duty" in the excavation of several of the critically important sites discussed here, in particular Leisey, Macasphalt Shell Pit, Haile 7C, and Haile 21A. The following individuals donated important specimens of vertebrate fossils to the UF collection from various Florida Blancan and Irvingtonian sites: Stephen Beck, D. J. Bethea, Lelia and William Brayfield, the late Howard H. Converse, Jr., Daniel Delgado, Ralph "Tony" Estevez, Wayne Filyaw, Frank A. Garcia, George Heslep, Mitchell Hope, Muriel Hunter, Eric Kendrew, the late Philip Kinsey, Larry Martin, Thomas Missimer, James Pendergraft, Brian Ridgway, Barbara Toomey, James Toomey, Reed Toomey, the late Benjamin I. Waller, Suzan Watts, and Steven Wilson. Field work at Leisey and Macasphalt and curation of vertebrate fossils from these and several other sites discussed here was supported by National Science Foundation Grants EAR 8708045, BSR 8314649 and BSR 8902822. This is University of Florida Contribution to Paleobiology Number 401.

ABBREVIATIONS

UF - Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville.

LF - Local Fauna.

NALMA - North American Land Mammal Age.

Ma - Mega-anna, millions of years before present on the radioisotopic time scale.

ka - kilo-anna, thousands of years before present on the radioisotopic time scale.

cm - centimeter.

m - meter.

km - kilometer.

T - Township.

R - Range.

P/p - upper/lower premolar (e.g. P4 is an upper fourth premolar).

M/m - upper/lower molar (e.g. m1 is a lower first molar).

Table 1. Vertebrate faunal list of the early Irvingtonian Leisey Shell Pit Local Fauna, Hillsborough County, Florida. This list has been compiled from the individual papers on the vertebrate groups published elsewhere in this volume. Within each family the genera and species are listed in alphabetical, not phylogenetic, order. Several species of amphibians and reptiles (Meylan, this volume) and birds (Emslie, this volume) are excluded from this list because they were identified only from Leisey 2 which contains a mixed assemblage of Irvingtonian and Rancholabrean taxa.

Chondrichthyes
- Batoidea
  - Pristidae
    - *Pristis* sp.
  - Dasyatidae
    - *Dasyatis*--2 species
  - Myliobatidae
    - *Aetobatus narinari*
    - *Myliobatis* sp.
    - *Rhinoptera bonasus*
  - Rhynchobatidae
    - *Rhynchobatus* sp.
- Galeomorpha
  - Orectolobidae
    - *Ginglymostoma cirratum*
    - *Ginglymostoma serra*
  - Odontaspidae
    - *Odontaspis taurus*
  - Lamnidae
    - *Carcharodon carcharias*
    - *Isurus hastalis*
    - *Isurus oxyrinchus*
  - Hemigaleidae
    - *Hemipristis serra*
  - Carcharhinidae
    - *Carcharhinus acronotus*
    - *Carcharhinus leucas*
    - *Carcharhinus limbatus*
    - *Carcharhinus obscurus*
    - *Carcharhinus plumbeus*
    - *Galeocerdo cuvieri*
    - *Negaprion brevirostris*
    - *Rhizoprionodon terraenovae*
    - *Sphyrna mokarran*

Osteichthyes
- Semionotiformes
  - Lepisosteidae
    - *Atractosteus spatula*
    - *Lepisosteus* cf. *L. oculatus*
    - *Lepisosteus osseus*

Table 1 Continued

- Amiiformes
  - Amiidae
    - *Amia calva*
- Elopiformes
  - Elopidae
    - *Elops saurus*
    - *Megalops atlanticus*
- Anguilliformes
  - Anguillidae
    - *Anguilla rostrata*
- Clupeiformes
  - Clupeidae
    - genus and species indet.
- Salmoniformes
  - Esocidae
    - *Esox* sp.
- Cypriniformes
  - Cyprinidae
    - *Notemigonus chrysoleucas*
  - Catostomidae
    - *Erimyzon* cf. *E. sucetta*
- Siluriformes
  - Ariidae
    - *Arius felis*
    - *Bagre marinus*
  - Ictaluridae
    - *Ameiurus natalis*
    - *Ameiurus nebulosus*
- Batrachoidiformes
  - Batrachoididae
    - *Opsanus* sp.
- Atheriniformes
  - Atherinidae
    - cf. *Menidia* sp.
  - Cyprinodontidae
    - *Cyprinodon variegatus*
    - cf. *Floridichthyes* sp.
    - *Fundulus* cf. *F. grandis*
    - *Fundulus seminolis*
    - *Fundulus majalis*
  - Exocoetidae
    - cf. *Hyporhamphus* sp.
- Perciformes
  - Carangidae
    - *Caranx hippos*
    - cf. *Trachinotus* sp.
  - Centrarchidae
    - *Lepomis* cf. *L. auritus*
    - *Lepomis gulosus*
    - *Lepomis microlophus*

Table 1 Continued

- *Micropterus salmoides*
- *Pomoxis nigromaculatus*
- Centropomidae
  - *Centropomus* sp.
- Ephippidae
  - *Chaetodipterus faber*
- Labridae
  - *Lachnolaimus maximus*
- Mugilidae
  - *Mugil* sp.
- Percichthyidae
  - cf. *Morone* sp.
- Sciaenidae
  - *Bairdiella* cf. *B. chrysoura*
  - *Cynoscion* cf. *C. nebulosus*
  - *Micropogonias undulatus*
  - *Pogonias cromis*
  - *Sciaenops ocellatus*
- Sparidae
  - *Archosargus probatocephalus*
  - *Calamus* sp.
  - *Lagodon rhomboides*
- Sphyraenidae
  - *Sphyraena barracuda*
- Pleuronectiformes
  - Bothidae
    - genus and species indet.
- Tetraodontiformes
  - Balistidae
    - *Balistes* sp.
  - Diodontidae
    - *Chilomycterus schoepfi*
    - *Diodon* sp.
  - Ostraciidae
    - *Lactophrys* sp.

Amphibia
- Urodela
  - Sirenidae
    - *Siren lacertina*
- Anura
  - Bufonidae
    - *Bufo* cf. *B. terrestris*
  - Ranidae
    - cf. *Rana* sp.

Reptilia
- Crocodylia
  - Alligatoridae
    - *Alligator mississippiensis*

Table 1 Continued

- Squamata
  - Lacertilia
    - Anguidae
      - *Ophisaurus compressus*
  - Serpentes
    - Boidae
      - cf. *Tropidophis* sp.
    - Colubridae
      - *Coluber* sp./*Masticophis* sp.
      - *Elaphe* cf. *E. obsoleta*
      - *Farancia* sp.
      - *Lampropeltis getulus*
      - *Nerodia* cf. *N. fasciata*
      - *Regina* cf. *R. alleni*
      - cf. *Thamnophis* sp.
    - Viperidae
      - *Agkistrodon piscivorous*
      - *Crotalus* cf. *C. adamanteus*
      - *Sistrurus miliarius*
  - Testudines
    - Cheloniidae
      - *Caretta caretta*[1]
      - *Chelonia mydas*
    - Chelydridae
      - *Chelydra serpentina*
      - *Macroclemys temminckii*
    - Testudinidae
      - *Gopherus polyphemus*
      - *Hesperotestudo crassiscutata*
      - *Hesperotestudo mlynarskii*
    - Emydidae
      - *Pseudemys* sp.
      - *Terrapene carolina*
      - *Trachemys scripta*
    - Kinosternidae
      - *Kinosternon* sp.
    - Trionychidae
      - *Apalone ferox*

- Aves
  - Gaviiformes
    - Gaviidae
      - *Gavia concinna*
      - *Gavia immer*
  - Podicipediformes
    - Podicipedidae
      - *Podiceps* sp.
      - *Podilymbus podiceps*

Table 1 Continued

- Pelecaniformes
  - Pelecanidae
    - *Pelecanus* cf. *P. erythrorhynchos*
  - Phalacrocoracidae
    - *Phalacrocorax*-2 species
  - Anhingidae
    - *Anhinga anhinga*
    - *Anhinga* sp.
- Ciconiiformes
  - Ardeidae
    - *Ardea* sp.
    - *Casmerodias albus*
    - *Egretta* cf. *E. tricolor*
  - Threskiornithidae
    - *Ajaia chione* new species
    - *Eudocimus leiseyi* new species
    - genus and sp. indet.
  - Ciconiidae
    - *Ciconia maltha*
    - *Ciconia* sp.
  - Teratornithidae
    - *Teratornis* cf. *T. incredibilis*
    - *Teratornis merriami*
  - Vulturidae
    - *Gymnogyps kofordi*
- Anseriformes
  - Anatidae
    - *Anabernicula gracilenta*
    - *Anas americana*
    - *Anas crecca*
    - *Anas platyrhynchos*
    - *Aythya affinis*
    - *Aythya americana*
    - *Aythya collaris*
    - *Aythya marila*
    - *Branta canadensis*
    - *Branta dickeyi*
    - *Bucephala albeola*
    - *Cygnus buccinator*
    - *Mergus serrator*
    - *Olor* sp.
    - *Somateria* cf. *S. spectabilis*
- Accipitriformes
  - Accipitridae
    - *Amplibuteo* sp.
    - *Aquila* sp.
    - *Buteo* cf. *B. lineatus*
    - *Buteo* sp.

Table 1 Continued

- Galliformes
  - Phasianidae
    - *Colinus* sp.
    - *Meleagris leopoldi/M. anza*
  - Gruiformes
    - Rallidae
      - *Fulica americana*
      - *Rallus* sp.
    - Gruidae
      - *Grus canadensis*
      - *Grus* sp.
  - Charadriiformes
    - Recurvirostridae
      - *Recurvirostra* sp.
    - Scolopacidae
      - *Limosa* cf. *L. fedora*
    - Alcidae
      - gen. et sp. indet.
    - Phoenicopteridae
      - *Phoenicopterus copei*
      - *Phoenicopterus ruber*
  - Strigiformes
    - Strigidae
      - *Bubo virginianus*
  - Passeriformes
    - Corvidae
      - *Corvus* sp.

- Mammalia
  - Xenarthra
    - Dasypodidae
      - *Dasypus bellus*
      - *Pachyarmatherium leiseyi* new genus and species
    - Pampatheriidae
      - *Holmesina floridanus*
    - Glyptodontidae
      - *Glyptotherium arizonae*
    - Megalonychidae
      - *Megalonyx wheatleyi*
    - Mylodontidae
      - *Paramylodon harlani*
    - Megatheriidae
      - *Eremotherium* n. sp.
      - *Nothrotheriops texanus*
  - Insectivora
    - Soricidae
      - *Blarina* cf. *B. carolinensis*
  - Carnivora
    - Canidae
      - *Canis armbrusteri*

Table 1 Continued

- *Canis edwardii*
- *Urocyon* sp.

Phocidae
- *Monachus tropicalis*

Procyonidae
- *Procyon* n. sp.

Ursidae
- *Arctodus pristinus*

Mustelidae
- *Mustela frenata*
- *Lutra canadensis*
- *Spilogale putorius*

Felidae
- *Homotherium* n. sp.
- *Lynx rufus*
- *Miracinonyx inexpectatus*
- *Smilodon gracilis*

Rodentia

Castoridae
- *Castoroides leiseyorum* new species

Geomyidae
- *Geomys pinetis*

Erethizontidae
- *Erethizon dorsatum*

Hydrochaeridae
- *Neochoerus* sp.

Muridae
- *Ondatra annectens*
- *Pedomys* n. sp.
- *Podomys* n. sp.
- *Sigmodon libitinus*
- *Synaptomys* sp.

Lagomorpha

Leporidae
- *Lepus* cf *L. townsendii*
- *Sylvilagus floridanus*

Perissodactyla

Tapiridae
- *Tapirus haysii*

Equidae
- *Equus "fraternus"*
- *Equus "leidyi"*
- *Equus (Hemionus)* n. sp.

Artiodactyla

Tayassudiae
- *Mylohyus fossilis*
- *Platygonus vetus*

Camelidae
- *Hemiauchenia macrocephala*[2]
- *Palaeolama mirifica*

Table 1 Continued

Cervidae
Odocoileus virginianus
Cetacea
Delphinidae
cf. *Stenella* sp.
cf. *Tursiops* sp.
genus and species indet.
Sirenia
Trichechidae
Trichechus sp.
Proboscidea
Mammutidae
Mammut americanum
Gomphotheriidae
Cuvieronius tropicus
Elephantidae
Mammuthus hayi

[1] Collected from Fort Thompson Formation above Leisey 1A bone bed.
2 Webb and Stehli (this volume) use *H. seymourensis* for the Leisey sample of *Hemiauchenia*.

DEFINITION OF CHRONOLOGIC AND BIOCHRONOLOGIC BOUNDARIES.

In this section, we discuss the age of the Pliocene/Pleistocene boundary and the subdivisions of the Pleistocene, as well as the definitions and subdivisions of the Blancan and Irvingtonian Land Mammal Ages used in this study. This is necessitated by recently published changes to the geologic and geomagnetic polarity time scales (Fig. 2). The Pliocene/Pleistocene boundary is now generally placed at 1.64 Ma, above the top of the Olduvai Normal Subchron of the Matuyama Chron (Berggren et al. 1985; Harland et al. 1990). This is younger than the 2.0 Ma date for this boundary recognized until recently by most North American vertebrate paleontologists (e.g. Kurtén and Anderson 1980). The older 2.0 Ma date was convenient because it also approximated the boundary between the Blancan and Irvingtonian Land Mammal Ages. With the recognition of a younger Pliocene/Pleistocene boundary, the earliest portion of the Irvingtonian (the interval between 2.0 and 1.6 Ma) is not Pleistocene as has been widely used, but rather latest Pliocene.

The Pleistocene Epoch is subdivided into the early, middle, and late Pleistocene (Fig. 2). The early Pleistocene begins at 1.64 Ma and ends at the boundary between the Matuyama and Brunhes chrons at 0.78 Ma. The middle

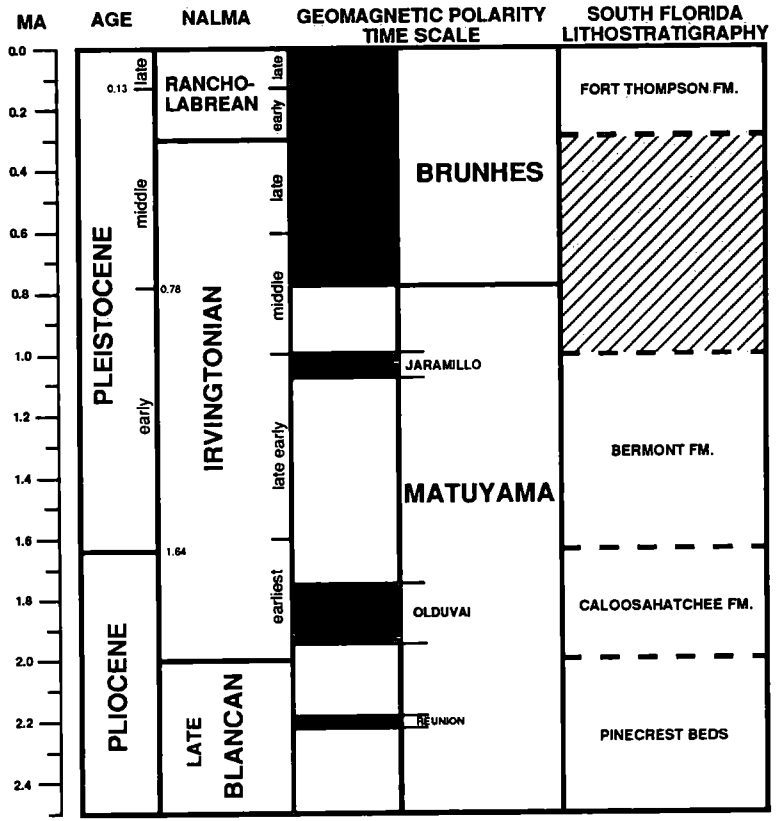

Figure 2. Chart depicting chronologic correlation between units of the geologic time scale (after Harland et al. 1990), North American Land Mammal Ages, the geomagnetic polarity time scale (after Valet and Meynadier 1993), and southwestern Florida stratigraphic formations.

Pleistocene covers the time period from the beginning of the Brunhes Chron at 0.78 Ma until the onset of the last (Sangamonian) interglacial at 132 ka. The late Pleistocene extends from about 132 ka to the Pleistocene/Holocene boundary at 10 ka. These subdivisions of the Pleistocene follow Harland et al. (1990), as adjusted for the up-dated geomagnetic polarity time scale of Valet and Meynadier (1993).

Vertebrate paleontologists do not all agree on the definitions and boundaries of the late Pliocene and Pleistocene North American Land Mammal Ages (NALMA), including part of the Blancan and all of the Irvingtonian and Rancholabrean. The subdivisions of these three NALMA are even less well understood. The two most recent attempts to define and subdivide the Irvingtonian and Rancholabrean (Lundelius et al. 1987-based on all mammal groups; Repenning 1987-based only on arvicoline rodents) are not in complete agreement.

Therefore, it is important to establish our criteria for defining and subdividing these NALMA, particularly the Irvingtonian since this is the age in which the Leisey Shell Pit LF occurs.

Repenning (1980; 1987) proposed a biochronology for the Blancan through the Rancholabrean NALMA based on evolutionary stages and immigration events of arvicoline rodents, more often termed "microtine" rodents in the extensive literature on the fossil history of this group. Our use of the term "arvicoline" in this paper is synonymous with the use of microtine by Repenning (1987) and other authors. Among the 74 Blancan and Irvingtonian arvicoline faunas discussed by Repenning (1987), only Cumberland Cave in Maryland is located in eastern North America (i.e., east of the Mississippi River). Repenning and Grady (1988) have since described an extensive middle Irvingtonian arvicoline fauna from Hamilton Cave, West Virginia. The published arvicoline fauna from the late Irvingtonian Coleman 2A LF, Sumter County, Florida (Martin 1974; Frazier 1977) was not mentioned by Repenning. Arvicolines are principally a temperate group of rodents, and consequently they have a limited distribution in subtropical regions such as Florida. With only three species presently occurring in the state, *Microtus pennsylvanicus*, *Pitymys pinetorum*, and *Neofiber alleni*, Florida has one of the poorest arvicoline faunas known from anywhere in the continental United States. Arvicoline rodents are unknown from Florida Blancan vertebrate faunas and are uncommon in most Pleistocene sites. Nonetheless, arvicolines are now known from eight Irvingtonian sites in Florida. A mammalian biochronology that uses many different types of taxa, in addition to arvicoline rodents (e.g., Lundelius et al. 1987), is much more applicable in Florida.

The Blancan NALMA covers the time interval between 4.5 and 2.0 Ma. Lundelius et al. (1987) divided the Blancan into the early, middle, and late Blancan, whereas Repenning (1987) recognized five Blancan subdivisions (Blancan I-V) based on arvicoline rodents. Only the late Blancan of Lundelius et al. (1987) or Blancan V of Repenning (1987) is discussed here, as early and middle Blancan (Blancan I-IV) land mammal faunas are unknown from Florida (Morgan and Ridgway 1987). The beginning of the late Blancan (about 2.5 Ma) was marked by the formation of the Panamanian Land Bridge and the first abundant appearance in North America of Neotropical immigrants, as well as the arrival of several genera of Eurasian immigrants. The late Blancan immigration events from both South America and the Old World probably were responses to major continental glaciation in the Northern Hemisphere and correspondingly low sea levels between about 3.0 and 2.5 Ma (Shackleton and Opdyke 1977).

Typical Blancan genera found in Florida faunas referred to this NALMA include *Borophagus, Trigonictis, Nannippus, Equus* (*Dolichohippus*), and *Rhynchotherium*. Neotropical mammalian genera that first appear in Florida during the late Blancan include the xenarthrans *Dasypus, Glyptotherium, Holmesina, Eremotherium*, and *Glossotherium* and the caviomorph rodents

Erethizon and *Neochoerus*, as well as the giant phororhacid bird *Titanis*. The co-occurrence or overlapping range zone of *Nannippus* and these South American immigrants defines a narrow time interval between 2.5 and 2.0 Ma, after the formation of the Panamanian isthmus and the beginning of the Great American Interchange, but before the extinction of *Nannippus* (Galusha et al. 1984; Lindsay et al. 1984; Morgan and Ridgway 1987).

The Blancan/Irvingtonian boundary is usually placed near the base of the Olduvai Subchron (Lundelius et al. 1987; Repenning 1987), that is now dated at 1.95 Ma (Valet and Meynadier 1993). Lundelius et al. (1987) did not precisely define this boundary on faunal grounds, but described a transitional period between about 2.0 and 1.6 Ma, during which late Blancan faunas gradually changed into early Irvingtonian faunas. However, Repenning (1987) noted a major change in arvicoline rodent faunas at the Blancan/Irvingtonian boundary (which he placed at 1.9 Ma), with the arrival of a number of Old World immigrants at this time, as well as the first abundant occurrence of taxa with unrooted teeth. The earliest Irvingtonian marks the first appearance of arvicoline rodents in the Florida fossil record (*Ondatra idahoensis*, *Atopomys salvelinus*). The ages of the late Blancan Borchers LF (Kansas) and earliest Irvingtonian Curtis Ranch LF (Arizona) are the primary basis for determining the date of the Blancan/Irvingtonian boundary (Lundelius et al. 1987:217). Borchers is located in the top of and just above the Pearlette B ash bed, which has a K-Ar date of 2.01 Ma (Izett 1981). Curtis Ranch stratigraphically lies just below the base of the Olduvai Subchron in geomagnetically reversed sediments. Valet and Meynadier (1993) show a date of about 1.95 Ma for the base of the Olduvai. These dates tightly constrain the boundary between the Blancan and Irvingtonian to the interval 2.01 to 1.95 Ma, or approximately 2.0 Ma (Fig. 2). A somewhat younger age for this boundary, 1.9 Ma, was used by Lundelius et al. (1987) and Repenning (1987), because the then accepted age for the base of the Olduvai Subchron was 1.88 Ma.

Lundelius et al. (1987) characterized the Irvingtonian by the first appearance of *Equus* sensu stricto (s.s.), *Euceratherium*, *Mammuthus*, *Smilodon*, and *Microtus*, among others. *Smilodon* is now known to be present in at least four late Blancan faunas in Florida (Berta 1987). *Mammuthus* does not reach North America from the Old World until sometime after 1.6 Ma, and thus its first appearance in the New World is well above the Blancan/Irvingtonian boundary (Lindsay et al. 1984; Lundelius et al. 1987). Since the Irvingtonian covers the latest Pliocene and much of the Pleistocene (between 2.0 and 0.3 Ma), it is useful to subdivide this NALMA into smaller time units. Lundelius et al. (1987) recognized three subages of the Irvingtonian: early Irvingtonian (Sappan), middle Irvingtonian (Cudahyan), and late Irvingtonian (Sheridanian). We use the terms early, middle, and late for these three subdivisions following the terminology generally applied to other NALMA (Woodburne 1987). We furthermore find it convenient to recognize four subdivisions of the Irvingtonian (earliest, late early, middle, and late), at least for

our biochronologic analyses of Florida fossil faunas. The boundaries between these four subdivisions of the Irvingtonian are not well constrained by geochronologic data in Florida, and thus should be considered approximate and provisional.

The boundary between the earliest and late early Irvingtonian is set at 1.6 Ma (Fig. 2), to approximate the Plio-Pleistocene boundary. At least some late early Irvingtonian faunas in Florida come from reversely magnetized sediments that are correlated to the portion of the Matayuma Chron between the Olduvai and Jaramillo Subchrons (between 1.79 and 1.07 Ma; Valet and Meynadier 1993). These faunas also most closely resemble those from the Great Plains (Gilliland, Holloman, Sappa) that are dated at 1.5 to 1.3 Ma (see discussion below).

The middle Irvingtonian of our usage is the equivalent of the Cudahyan Subage of Lundelius et al. (1987), and approximates the Irvingtonian II of Repenning (1987). In the Great Plains, Cudahyan faunas underlie the Pearlette O ash (0.61 Ma; Izett 1981) and overlie the Pearlette S ash (1.27 Ma; Izett 1981). The oldest faunas included in the middle Irvingtonian were deposited during the portion of the Matayuma Chron that postdates the Jaramillo, an interval now dated at 0.99 to 0.78 Ma (Valet and Meynadier 1993). These include portions of the Alamosa LF of Colorado (Rogers et al. 1985), and the Irvington LF and Centerville Beach LF of California (Lindsay et al. 1975; Repenning 1987). We therefore suggest that the age of the top of the Jaramillo Subchron, ca. 1.0 Ma, be used as the boundary between the early and middle Irvingtonian. The Cudahy LF of Kansas is associated with the 0.61 Ma Pearlette O ash, and thus forms a convenient upper boundary for the middle Irvingtonian (Lundelius et al. 1987).

The late Irvingtonian (or Sheridanian) includes faunas younger than 0.6 Ma, but which predate the dispersal of *Bison* into North America, the event that defines the base of the Rancholabrean. Unfortunately, this dispersal event is poorly constrained, and estimated to lie between 0.5 and 0.2 Ma (Lundelius et al. 1987). We therefore use the approximate midpoint of this range, 0.3 Ma, for the Irvingtonian/Rancholabrean boundary, with the expectation that furture work will more precisely document the arrival of *Bison* in North America. The 0.3 Ma date also corresponds to the beginning of the late middle Pleistocene, and the onset of a major period of continental glaciation (Richmond and Fullerton 1986).

GEOLOGY AND GEOCHRONOLOGY OF THE LEISEY SHELL PITS

Geologic Descriptions of Leisey Strata.--Sediments exposed by mining operations at the Leisey Shell Pit are tentatively referred to four formations, each of which has produced vertebrate fossils, as well as a surficial layer of unconsolidated sand (Fig. 3). In this section we first describe the local geology and stratigraphy of the three Leisey Shell pits, particularly Leisey 1 and 3, emphasizing the bone-rich

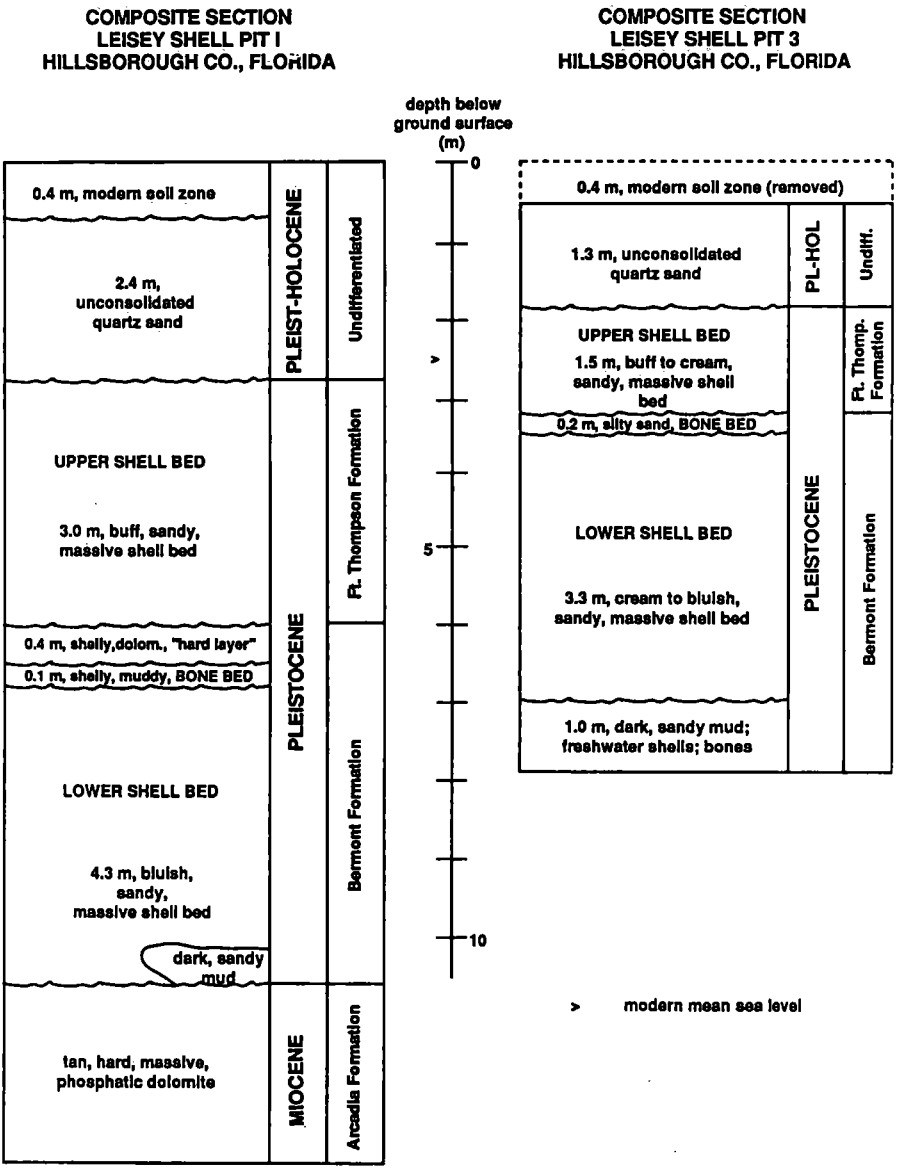

Figure. 3. Stratigraphic sections of the Leisey Shell Pit 1A and 3A sites, Hillsborough County, Florida, measured by the authors in 1984 and 1986. See text for detailed description of the sections.

lenses. We then summarize the geochronology of the Leisey strata based on vertebrate biochronology and data from other papers in this volume, including invertebrate biostratigraphy, paleomagnetics, and strontium isotope stratigraphy.

At the base of the stratigraphic section exposed in the Leisey Shell pits is a well-indurated, tan to light gray, clayey, phosphatic dolostone. Identifiable invertebrate fossils have not been recovered from this unit, but waterworn sirenian and cetacean fossils are fairly common. The top of this unit is very uneven and represents a major erosional unconformity. The most biostratigraphically-useful fossil found in this bed is a well preserved, slightly worn lower molar (m1 or m2) of a merychippine-grade horse (UF 53819). The crown height and enamel pattern of UF 53819 closely matches those of lower molars recovered from the Arcadia Formation at Nichols Mine in Polk County, located about 35 km northeast of Leisey. Hulbert and MacFadden (1991) tentatively referred this sample to "*Merychippus*" *tertius*, a species otherwise known from the late Hemingfordian (late early Miocene) of Nebraska. However, other mammals in the Nichols Mine fauna, principally rodents, indicate a slightly younger, very early Barstovian (earliest middle Miocene) age (Pratt, Morgan, and Poyer in prep.). Scott (1988) stated that the Arcadia Formation is widespread throughout the subsurface of southern Florida, including southwestern Hillsborough County, and his description of its lithology agrees well with that of the basal Leisey stratum. Accordingly, the lowermost bed at Leisey is referred to the Arcadia Formation of the Hawthorn Group.

The Bone Valley Formation unconformably overlies the Arcadia Formation over a wide area in central Florida (Scott 1988). We use the name Bone Valley Formation in its traditional, broad sense, and as the equivalent of the Bone Valley Member of the Peace River Formation of Scott (1988). As mapped in the subsurface by Scott (1988, figs. 36, 53), the Bone Valley Formation rapidly thins in western Hillsborough and Manatee counties, and is absent in some sections. The Bone Valley Formation was not observed in outcrop at Leisey, but several land mammals characteristic of this unit were recovered from a reworked zone on top of the Arcadia Formation at the north end of Leisey Pit 1 (Fig. 1). This site, called Leisey 1C, contained phosphate pebbles and gravel and spheroidal metaquartzite pebbles, all typical of the uppermost unit of the Bone Valley Formation (Pirkle et al. 1967). Vertebrate fossils from Leisey 1C are heavily waterworn and a dull black color. Their preservation differs considerably from bones recovered from the overlying shell beds. Both marine and terrestrial taxa are represented (Hulbert and Morgan 1989). As is typical in low-elevation deposits of the Bone Valley Formation in southwestern Florida, isolated horse teeth are the most common terrestrial vertebrate fossils, and the most useful biochronologically.

Three equid species are recognized from Leisey 1C on the basis of diagnostic dental character states: *Nannippus aztecus* (UF 43564, 107531, 107532; see Hulbert 1990 for use of *N. aztecus* instead of *N. minor*); *Neohipparion eurystyle*

(UF 107528); and *Cormohipparion ingenuum* (UF 107529, 107530). The chronologic range of the first two species is late early Hemphillian through very late Hemphillian (7.0 to 4.5 Ma; Hulbert 1987, 1990). The range of the latter is early Clarendonian through late early Hemphillian (11.5 to 6 Ma; Hulbert 1988b). Their concurrent range is thus constrained to the late early Hemphillian (very late Miocene). Similarly preserved, low-elevation occurrences of fossiliferous Bone Valley-type deposits are also known from Manatee (Port Manatee, Manatee County Dam, and Braden River sites) and Sarasota (Lockwood Meadows) counties. Based on the biochronology of their equid faunas these five Gulf Coastal sites, termed the Manatee Fauna (Morgan 1994), are correlated with the late early Hemphillian (approximately 7 Ma) Withlacoochee 4A and Moss Acres local faunas from Marion County in northern Florida (Hulbert 1988b), and were probably deposited just prior to the latest Miocene (Messinian) eustatic drop in sea level that occurred between 6.7 and 5.2 Ma (Webb and Tessman 1968; Haq et al. 1987; Morgan 1994). Leisey 1C represents the northernmost occurrence of these low elevation, Bone Valley-type deposits along the Florida Gulf Coast.

A rostral or mandibular fragment of the long-beaked dolphin *Pomatodelphis* (UF 142238) and four auditory bullae of small cetotheriid mysticetes (UF 88614, 107524, 142240, 142246) from Leisey 1 closely resemble specimens from middle and late Miocene sites elsewhere in peninsular Florida, in particular the lower unit of the Bone Valley Formation of Polk and adjacent counties (Morgan 1994). Abundant large, dense sirenian ribs (UF 142241-142243) from Leisey 1 probably pertain to the dugongid *Metaxytherium*, although the ribs are not specifically diagnostic. The Leisey marine mammal fossils were found near the base of the section in the Leisey 1 Pit, but were collected out of stratigraphic context and thus could conceivably belong to either the Barstovian or Hemphillian faunas. The *Metaxytherium-Pomatodelphis*-cetothere assemblage (Morgan 1994) characterized Florida marine mammal faunas from the late early Miocene (late Hemingfordian) through the late Miocene (late early Hemphillian).

An approximately 8 m thick sequence of massive marine shell beds rests upon the eroded surface of the Arcadia Formation at Leisey (Fig. 3). Reworked pebbles and cobbles of dolostone and phosphate from the underlying Arcadia Formation are common in the base of the shell bed sequence. The shell beds consist primarily of well preserved mollusc shells in an unconsolidated matrix of fine quartz sand. In Leisey Shell Pit 1 there are two major superposed shell beds separated by an erosional unconformity, and locally by a thin layer of indurated freshwater limestone. These two units are informally designated the lower and upper shell beds, respectively (Fig. 3). The upper and lower shell beds are similar lithologically, but differ in the composition of their molluscan faunas (Portell et al. 1992) and by the presence of dark organic-rich silt and clay lenses in the lower shell bed. The size, stratigraphic position, and faunal composition of these lenses varies throughout the Leisey pits. All of the major vertebrate concentrations

(Leisey 1A, 1B, 3A, and 3B) originate from these organic lenses. One common type of organic unit encountered in the Leisey pits is composed of a mixture of dark organic clay and silt, fine to medium-grained sand, well preserved freshwater mollusc shells (e.g. the gastropods *Viviparus* and *Planorbella* and unionid bivalves), and locally abundant fossil wood. Other organic lenses consist primarily of shells of the estuarine bivalves *Rangia* or *Crassostrea*. The most extensive of these organic units, Leisey 3B, is not actually a lens but consists of a layer of very dark-colored clay and silty clay from 20 cm to over 1 m in thickness occurring widely throughout Leisey Pit 3. Vertebrate fossils are sometimes locally abundant in Leisey 3B, but were never concentrated to the extent seen in the two main "bone beds" (Leisey 1A and 3A).

Leisey 1A, the largest and most thoroughly studied organic unit in the lower shell bed, occurs higher in the section than most of these lenses (approximately 4.5 m above the top of the Arcadia Formation, Fig. 3), and differs from them in containing predominantly marine molluscs. Leisey 1A varies in thickness from 5 to 30 cm over an area of about 2000 m^2. It consists of an unconsolidated, poorly sorted mixture of well preserved mollusc shells, vertebrate bones and teeth, fossilized mangrove root casts, fine-grained quartz sand, silt, and dark brown mud. The deposit thins gradually towards its margins, with vertebrate remains becoming increasingly scarce. Leisey 1A is often referred to as a "bone bed" because of the tens of thousands of vertebrate fossils it contained, although volumetrically, marine mollusc shells comprised most of the deposit. The taxonomic composition of the Leisey 1A marine molluscs is generally similar to that of the main lower shell bed (Portell et al. 1992). The freshwater molluscs of Leisey 1A, in contrast to those found in the lower organic lenses, often show signs of transport damage. The mangrove roots probably were not contemporaneous with the deposition of the Leisey 1A shells and vertebrate fossils, but more likely grew down through the sediments at a later date. This explains the absence of mangrove pollen in the Leisey 1A sediments (Rich and Newsom this volume).

Immediately above the Leisey 1A bone bed, and separated from it by a poorly defined unconformity, is a 30 to 50 cm thick layer of fossiliferous, indurated, calcareous freshwater limestone. This layer extends beyond the boundaries of Leisey 1A, locally separating the lower and upper shell beds. The limestone contains great numbers of freshwater gastropod shells (especially *Planorbella scalaris*), some poorly preserved and apparently reworked marine mollusc shells, fine-grained quartz sand, and rare bones. The vertebrate fossils pertain almost exclusively to freshwater taxa such as emydid and trionychid turtles, alligators, and water birds. The fauna suggests a freshwater origin for the limestone. Such freshwater "marls" are commonly interbedded with marine strata in the Plio-Pleistocene stratigraphic sequence in southern Florida (e.g. DuBar 1958, 1962).

An erosional unconformity above the indurated calcareous marl separates it from the upper marine shell bed. Reworked fragments of the marl are present in

the base of the upper shell bed. Like the lower shell bed and bone bed, the upper shell bed lacks distinct bedding and is composed predominantly of marine mollusc shells. However, in contrast to the bone bed, the upper shell bed has few freshwater gastropods, is nearly devoid of bones, lacks fossilized mangrove roots, and has a higher percentage of fine-grained sand and a lower percentage of silt and clay. The only notable vertebrate fossils from the upper shell bed in the Leisey 1 pit are a partial plastron of the loggerhead sea turtle, *Caretta*, and a tooth and vertebra of *Bison*. Overlying the upper shell bed is a 2.4 m thick layer of massive unconsolidated Quaternary quartz sand containing no fossils.

Leisey 1B is a small vertebrate site located several hundred meters south of Leisey 1A and about 3 m lower in the stratigraphic section. The bones occurred in a thin lens at the base of the lower shell bed not far above the contact with the underlying Arcadia Formation. Some of the vertebrate fossils were collected from a rubble zone lying directly on top of the eroded surface of the Arcadia Formation. Based on the limited vertebrate assemblage present, the fauna from Leisey 1B is very similar to that of Leisey 1A. The most diagnostic mammals present in Leisey 1B are the glyptodont *Glyptotherium arizonae*, the giant armadillo *Holmesina floridanus*, the giant tapir *Tapirus haysii*, and the primitive mammoth *Mammuthus hayi*, all indicative of a late early Irvingtonian (early Pleistocene) age.

Leisey 3A occupied about one fourth the area of Leisey 1A. It too is located stratigraphically high within the lower shell bed (Fig. 3). It differs from Leisey 1A in containing a very limited large terrestrial vertebrate fauna overwhelmingly dominated by juvenile individuals of the llama, *Hemiauchenia macrocephala*, many of which consist of associated skeletons. Leisey 3A has a considerably richer and more diverse terrestrial and freshwater microvertebrate fauna than Leisey 1A. The most common taxa in the molluscan fauna are the brackish water bivalve *Rangia* and the freshwater gastropod *Viviparus*. No indurated freshwater marl layer separates Leisey 3A from the overlying shell bed, nor are mangrove roots present as in Leisey 1A.

Regional Stratigraphic Correlation.--The Pliocene and Pleistocene stratigraphy of southern Florida is currently undergoing intensive study by a large number of geologists and paleontologists (e.g. Lyons 1991; DuBar et al. 1991; Scott and Allmon [eds.] 1992). Clearly, there will be many changes in the nomenclature of the geologic units recognized in this region (e.g. Waldrop and Wilson 1990; DuBar at al. 1991; Scott 1992). It is not our intention here to revise the stratigraphic nomenclature of South Florida, since we are not stratigraphers, nor do we study molluscs, the primary fossil group upon which the southern Florida biostratigraphic sequence is based. Our goal is to place the stratigraphic section exposed in the Leisey Shell Pit into the currently recognized stratigraphic framework for the region to insure that our work will be comprehensible to present and future workers. Lyons (1991) has recently summarized the biostratigraphic

basis for recognizing the various formational units withing the Plio-Pleistocene shell beds in southern Florida. We follow his subdivision and characterization of these geologic units.

A century of geologic and paleontologic investigation has resulted in a generally agreed upon stratigraphic sequence for the extensive Pliocene and Pleistocene shell beds of southern Florida (e.g. DuBar 1974; Lyons 1991), although see Scott (1992) for an alternative view. On the basis of stratigraphic superposition there is little disagreement that the relative ages of the units in question are (from oldest to youngest): Pinecrest Beds (also known as the Pinecrest Sand Member of the Tamiami Formation of Hunter 1968; the Fruitville Formation of Waldrop and Wilson 1990; and the Myakka Member of the Sarasota Formation of DuBar et al. 1991), Caloosahatchee Formation, Bermont Formation, Fort Thompson Formation, and Coffee Mill Hammock Formation (Fig. 2). These strata are often similar in their lithological composition, generally consisting of abundant shells of marine molluscs in a matrix of unconsolidated fine quartz sand, but also including beds of calcareous marl, indurated freshwater limestone, and dark organic-rich silts and clays. These lithologies reflect a diversity of nearshore marine, estuarine, and freshwater depositional environments.

The southern Florida formations composed predominantly of marine shell beds are primarily differentiated on the basis of the composition of their molluscan faunas. As suggested by many previous workers, these formations are perhaps more properly regarded as biostratigraphic units (biozones) because the North American Stratigraphic Code (1983) requires that formal lithostratigraphic units be differentiated on the basis of lithology, not fossil content. In the absence of a formally proposed, well documented biostratigraphic nomenclature for Plio-Pleistocene units in southern Florida, such as that proposed for the middle Atlantic Coastal Plain by Blackwelder (1981a), we continue to follow current geological usage in discussing these units (e.g. Lyons 1991).

The presence of stratigraphically restricted species of molluscs has until recently been the primary method used to correlate geologic units in southern Florida. The percentage of extinct species of molluscs in a fauna, termed the "Lyellian percentage," is another method that has been used to determine relative age among Florida shell beds. Portell et al. (1992, this volume) identified more than 200 species of molluscs from the lower shell bed and bone bed from Leisey Shell Pit 1, approximately 3% of which are extinct. Previously published estimates of 10-12% extinct species of molluscs from Leisey (Hulbert and Morgan 1989; Webb et al. 1989) were based upon a preliminary analysis of the molluscan fauna and are now known to be too high. The Lyellian percentage of extinct species of molluscs from Leisey is intermediate between faunas of the Bermont and Ft. Thompson formations (DuBar 1974; Lyons 1991). Bermont molluscan faunas typically contain from 10-20% extinct species (Hoerle 1970; DuBar 1974; Stanley 1986), compared to those from the younger Fort Thompson Formation which are

composed of fewer than 5% extinct taxa. The Caloosahatchee Formation, which directly underlies the Bermont Formation, contains from 50 to 65% extinct species of molluscs (Olsson and Harbisson 1953; Stanley 1986; Lyons 1991).

DuBar (1958) suggested that the Caloosahatchee Formation was late Pleistocene in age based primarily on evidence from vertebrate fossils. He later regarded the Caloosahatchee to be early and middle Pleistocene (1974), whereas DuBar et al. (1991) placed the Caloosahatchee in the early Pleistocene. We have re-examined the small sample of mammalian fossils (*Holmesina*, *Eremotherium*, advanced *Equus*, and *Palaeolama*) reported from the Caloosahatchee Formation by DuBar (1958; 1974). These taxa indicate a latest Pliocene or Pleistocene age (i.e. Irvingtonian or Rancholabrean) but, with the possible exception of the *Holmesina*, are not sufficiently diagnostic to provide a more specific indication of the age. The size of several *Holmesina* osteoderms collected by DuBar from the Caloosahatchee Formation is suggestive of a latest Pliocene or early Pleistocene (early Irvingtonian) age. Within the past five years, an extensive vertebrate fauna has been collected from the Caloosahatchee Formation in the De Soto Shell Pit in De Soto County. Preliminary analysis of the De Soto Shell Pit vertebrate fauna (see discussion below and Table 2) suggests correlation with the well known latest Pliocene (earliest Irvingtonian) Inglis 1A LF of northern Florida. Lyons (1991) also considered the Caloosahatchee Formation to be very late Pliocene in age on the basis of its molluscan fauna.

DuBar (1974) originally proposed the Bermont Formation as an informal unit, but distinguished the Bermont Formation from the underlying Caloosahatchee Formation primarily by the absence of most typical Caloosahatchee molluscs, and by the presence of a few species that are restricted to the Bermont. DuBar (1974) specifically noted that these two units were similar lithologically. Among the species of molluscs unique to the Bermont formation (McGinty 1970; DuBar 1974; Lyons 1991), only the gastropod *Strombus mayacensis* has been identified from Leisey (Portell et al. 1992). The lower shell bed at Leisey (including vertebrate sites Leisey 1A and 3A) is tentatively referred to the Bermont Formation on the basis of compatible lithology, faunal similarity, and the presence of seven extinct invertebrate taxa (see Portell et al. this volume). In his original description of the Bermont Formation, DuBar (1974) noted that it was found in widely scattered exposures from Charlotte County north to Levy County along the West Coast, and in the vicinity of Lake Okeechobee on the Atlantic Coast.

The best known Bermont molluscan faunas occur 100 km or more south of Leisey in Charlotte, Glades, Hendry, and Palm Beach counties. The Belle Glade Rock Pit in Palm Beach County (Hoerle 1970; McGinty 1970), perhaps the best known Bermont locality, contains over twice the number of molluscan species as Leisey of which approximately 15% are extinct (Hoerle 1970; Lyons 1991). However, the fossils from the Belle Glade Rock Pit were collected entirely from spoil piles, and thus may contain a mixture of faunas (Lyons 1991). The vast

majority of the Leisey molluscs were collected from in-place stratigraphic sections. The reduced number of extinct species at Leisey suggests that its molluscan fauna may be somewhat younger than other Bermont faunas, and as such is intermediate in age between this unit and faunas of the Fort Thompson Formation.

Geochronology of the Leisey Shell Pit Beds.–In this section we review previous attempts to date the Bermont and Fort Thompson formations, and briefly summarize paleomagnetic (see MacFadden this volume) and stable strontium isotope (see Jones et al this volume) data from Leisey. The Leisey Shell Pit provides an important cross-reference point for biochronologies based on marine molluscan assemblages (e.g., Blackwelder 1981a) and terrestrial mammals (North American Land Mammal Ages, e.g., Savage and Russell 1983; Woodburne 1987). Biostratigraphic data from various microfossil groups present in the Leisey strata (e.g., foraminifera, ostacodes, calcareous nannoplankton) have not yet been analyzed.

Prior to the 1960s, beds now referred to the Bermont Formation were usually considered the uppermost strata of the Caloosahatchee Formation (DuBar 1958; 1962). The Bermont Formation was proposed as an informal name in its original description (DuBar 1974), but has received widespread use in subsequent publications (e.g. Lyons 1991; DuBar et al. 1991) and was listed as a valid unit in Swanson et al. (1981). Strata placed in the Bermont Formation by DuBar (1974) have variously been referred to as Unit F (DuBar 1962), Unit A (Olsson 1964), Glades Unit (Hoerle 1970; McGinty 1970), the Belle Glade Member of the Fort Thompson Formation (Hunter 1968), and the Okeechobee Formation (Scott 1992).

There are two prevailing opinions among invertebrate paleontologists regarding the age of the Bermont Formation. DuBar (1974), Petuch (1988), and DuBar et al. (1991) considered the Bermont to be middle Pleistocene, falling between 0.6 and 0.3 Ma. Although Blackwelder (1981b) placed the Bermont in the late Pleistocene, he did not recognize a three-part subdivision of the Pleistocene. His proposed age of approximately 0.5-0.4 Ma for the Bermont Formation would place this unit in the middle Pleistocene as recognized here. Evidence for a middle Pleistocene age comes primarily from the results of amino acid racemization studies (Mitterer 1975), from the stratigraphic position of the Bermont between the supposedly early Pleistocene Caloosahatchee and late Pleistocene Fort Thompson (DuBar et al. 1991), and indirectly through correlation with the Canepatch Formation (Oaks and Dubar 1974; Blackwelder 1981a,b; DuBar et al. 1991). Other invertebrate paleontologists (e.g. Hoerle 1970) have regarded the Bermont as either late Pliocene or early Pleistocene, citing little evidence beyond the Lyellian percentage of 10 to 25% extinct species of molluscs. Bender (1973) obtained dates ranging from 1.9-1.75 Ma for the Caloosahatchee Formation using the He/U method on corals, which, if accurate, would constrain the overlying Bermont Formation as younger than 1.7 Ma.

Oaks and DuBar (1974) correlated the Bermont Formation with the Canepatch Formation of North and South Carolina. The Canepatch is a relatively securely dated deposit, assigned a middle Pleistocene age on the basis of a uranium-series date of 460±100 ka (Szabo 1985), normal geomagnetic polarity, and ostracode biochronology (Cronin 1980). Blackwelder (1981a,b) placed the age of the Canepatch Formation between 0.5 and 0.4 Ma, assigning it to the Myrtlean Substage of the Longian Stage. Longian Stage molluscan assemblages contain an essentially modern fauna with less than 5% extinct species. Blackwelder (1981a), citing Oaks and DuBar's (1974) correlation of the Canepatch and Bermont, also placed the Bermont in his Myrtlean Substage. Despite these previous age estimates, several lines of evidence indicate that the Bermont is substantially older than the Canepatch.

Geochronological data derived from magnetic polarity, strontium isotope stratigraphy, sea level, and vertebrate chronology are very useful in helping to determine the age of the Bermont Formation at the Leisey Shell Pit. Samples for paleomagnetic study were taken through a 5 m section at Leisey, including samples bracketing the vertebrate-bearing lenses Leisey 1A, 3A, and 3B. All sediments from both the Leisey 1A and Leisey 3A sites are of reversed magnetic polarity and lie within the Matuyama Chron (Webb et al. 1989; MacFadden this volume). The boundary between the Matuyama Chron of generally reversed polarity and the Brunhes Chron of normal polarity is 0.78 Ma (Cande and Kent 1992; Valet and Meynadier 1993). The Canepatch Formation of the Carolinas is geomagnetically normal (Cronin 1980), and thus is not synchronous with the reversed sediments from Leisey.

Leisey could correlate with the latest Matuyama, between 0.99 and 0.78 Ma, but other evidence argues against this hypothesis. Most of the uppermost zone of the Matuyama Chron corresponds with two periods of continental glaciation (glaciations F and G of Richmond and Fullerton 1986). However, the two Leisey sites were deposited very close to current sea level and thus would not correlate with a glacial interval characterized by signficantly lowered sea levels. Furthermore, the marine molluscan fauna from Leisey does not contain evidence of cooler water forms (Portell et al. 1992). The interval between 1.55 and 1.0 Ma was a warm period lacking major glacial episodes (Richmond and Fullerton 1986). Ratios of stable strontium isotopes from biogenic carbonate (shells of the marine bivalve *Chione cancellata*) from the Bermont Formation at Leisey correspond to ages of 2.08 Ma for Leisey 1A and 1.33 Ma for Leisey 3A (Jones et al this volume). When the 95% confidence intervals for the Leisey strontium isotope values (±0.56 Ma) are taken into consideration, Leisey 1A could be as young as 1.52 Ma and Leisey 3A could be as old as 1.89 Ma, yielding a possible overlap of almost 0.4 Ma between the two sites. Vertebrate biochronology, as discussed in detail below, favors a late early Irvingtonian age (1.6-1.0 Ma) for the Bermont at Leisey.

In summary, both mammalian biochronology and geochronological data indicate that the Leisey Shell Pit LF is early Pleistocene in age, about 1.6 to 1.0 Ma. Faunal criteria strongly suggest that Leisey is younger than latest Pliocene faunas such as Inglis 1A and De Soto Shell Pit (i.e., younger than 1.6 Ma) and older than the late middle Irvingtonian McLeod Limerock Mine LF (older than 0.7 Ma). Biochronological data restrict the age of Leisey to the latter half of the early Irvingtonian or the first half of the middle Irvingtonian. Of these two possiblities the mammalian fauna is more suggestive of an early Irvingtonian age. Geochronological data also rule out an early middle Irvingtonian age (between 1.07 and 0.78 Ma). The similarity of Leisey to certain middle Irvingtonian vertebrate faunas suggests that Leisey falls late in the early Irvingtonian, and accordingly may be no more than several hundred thousand years older than Cumberland Cave, Port Kennedy Cave, Hamilton Cave, and other early middle Irvingtonian faunas. The best estimate for the age of the Bermont Formation at the Leisey Shell Pit, taking into account all chronologic indicators, is between 1.55 and 1.1 Ma. Moreover, it is most likely that the Leisey 1A and 3A vertebrate sites are less than 1.3 Ma.

In contrast to the Bermont Formation, there has been relatively little disagreement concerning the age of the Fort Thompson Formation. Most evidence points to a middle or late Pleistocene age. In particular, the Coffee Mill Hammock Member of the Fort Thompson Formation or Coffee Mill Hammock Formation of some authors is rather securely correlated with the last major interglacial (Sangamonian) between 130-120 ka (DuBar 1974; Mitterer 1975; Lyons 1991). This was the last time sea level rose substantially higher than present levels (Bloom 1983). DuBar (1958:135) listed 13 vertebrate taxa collected *in situ* in the Fort Thompson Formation. Contrary to his claims, none of these taxa are strictly limited to the late Pleistocene (Rancholabrean) as currently understood (Kurtén and Anderson 1980; Lundelius et al 1987; Repenning 1987). A late Irvingtonian age is also possible on faunal grounds alone.

Several specimens of *Bison* were collected *in situ* from the upper shell bed at Leisey Pit 1, which has been referred to the Fort Thompson Formation based on the lack of extinct species in the molluscan fauna. The occurrence of *Bison* essentially defines the Rancholabrean Land Mammal Age (Lundelius et al. 1987). *Holmesina septentrionalis, Sigmodon hispidus*, and *Tapirus veroensis* all were collected from spoil in Leisey Pit 2, but are presumed to have been derived from the upper shell bed, as they were not recovered from the lower shell bed at Leisey despite intensive sampling. Among these three species, *Sigmodon hispidus* is characteristic of late Rancholabrean faunas in Florida, whereas the latter two species occur in both late Irvingtonian and Rancholabrean faunas (<0.6 Ma). However, the overlapping range zone for these three species plus *Bison*, occurs only during the Rancholabrean (0.3-0.12 Ma). Vertebrate fossils from Leisey support previous determinations that at least the upper units of the Fort Thompson Formation are

late middle or late Pleistocene in age.

There is a significant gap, corresponding to most of the middle Pleistocene, between our proposed upper limit for the Bermont beds at the Leisey Shell Pit of about 1.0 Ma and strata of the Fort Thompson Formation containing *Bison* that are 0.3 Ma or younger. There are presently no middle or late Irvingtonian vertebrate faunas known from Florida that occur in stratigraphic superposition with marine geologic units.

VERTEBRATE BIOCHRONOLOGY OF THE LEISEY SHELL PIT LOCAL FAUNA

Plio-Pleistocene vertebrate biochronology in Florida.—Table 2 shows the chronological distribution of 128 species of mammals in Florida during the late Pliocene and Pleistocene. Five Blancan and 11 Irvingtonian vertebrate faunas are listed separately in Table 2, whereas the early and late Rancholabrean are presented as composite faunas derived from a number of different sites. This table does not include all of the Blancan and Irvingtonian sites known from Florida, only those with the largest and most chronologically significant faunas, arbitrarily defined as faunas containing 10 or more species of mammals. Several other important Florida Blancan and Irvingtonian sites that contain age-diagnostic mammals are discussed in the text. We caution that Table 2 does not provide complete mammalian faunal lists for the individual sites, but includes only those species we consider to be biochronologically diagnostic in Florida. For example, Insectivora, Chiroptera (with the exception of *Desmodus*), and many species of Rodentia are not included in Table 2, although these groups are often common members of the faunas listed.

We emphasize that the data presented here are based primarily on Florida faunas and therefore, in the case of certain taxa, may not have widespread applicability to other North American vertebrate faunas of similar age. Examples include the late Blancan arrival in Florida of the armadillos *Dasypus* and *Holmesina* and the giant ground sloth *Eremotherium*, all of South American origin. These three genera have not been reported elsewhere in North America prior to the Irvingtonian. Another Neotropical immigrant, the huge flightless bird *Titanis walleri*, is unknown outside of Florida, yet its chronological range is restricted to the late Blancan and earliest Irvingtonian, and it is thus an excellent biostratigraphic indicator within the state. Whenever possible we attempt to correlate Florida vertebrate faunas with faunas elsewhere in North America, especially in instances where the non-Florida faunas have been radiometrically dated or can be correlated to the magnetic polarity time scale.

Table 2. Biochronological distribution of Blancan, Irvingtonian, and Rancholabrean mammals in Florida. An "X" indicates a definite identification, "?" a possible identification, and "–" an absence.

	Late Blancan (2.5-2.0 Ma)					Earliest Irvingtonian (2.0-1.6 Ma)	
	Santa Fe River 1	Haile 15A	Macasphalt Shell Pit	Kissimmee River	Haile 7C	Inglis 1A	De Soto Shell Pit
Didelphis virginiana	–	–	–	–	–	–	–
Dasypus bellus	X	X	X	X	X	X	X
Holmesina floridanus	X	X	X	X	X	X	X
Holmesina septentrionalis	–	–	–	–	–	–	–
Glyptotherium arizonae	X	–	–	X	X	X	X
Glyptotherium floridanum	–	–	–	–	–	–	–
Pachyarmatherium leiseyi	–	–	–	X	–	–	–
Glossotherium chapadmalense	X	X	X	X	–	–	–
Paramylodon harlani	–	–	–	–	–	X	–
Megalonyx jeffersonii	–	–	–	–	–	–	–
Megalonyx leptostomus	X	–	X	X	X	X	X
Megalonyx wheatleyi	–	–	–	–	–	–	–
Eremotherium mirabile	–	–	–	–	–	–	–
Eremotherium n. sp.	–	–	–	?	X	X	X
Nothrotheriops texanus	–	–	–	–	–	–	–
Desmodus archaeodaptes	–	–	–	–	–	X	–
Desmodus stocki	–	–	–	–	–	–	–
Borophagus diversidens	X	–	–	–	–	–	–
Canis armbrusteri	–	–	–	–	–	–	–
Canis dirus	–	–	–	–	–	–	–
Canis edwardii	–	–	–	–	–	X	X
Canis latrans	–	–	–	–	–	–	–
Canis lepophagus	X	–	?	–	–	–	–
Urocyon cinereoargenteus	–	–	–	–	–	–	–
Urocyon minicephalus	–	–	–	–	–	–	–
Urocyon n. sp.	–	–	–	–	–	X	–
Procyon lotor	–	–	–	–	–	–	–
Procyon n. sp.	?	–	?	?	–	X	X
Arctodus pristinus	X	–	–	X	–	X	–
Tremarctos floridanus	–	–	–	–	–	–	–
Conepatus leuconotus	–	–	–	–	–	–	–
Conepatus robustus	–	–	–	–	–	–	–

Table 2 Extended.

Late Early Irvingtonian (1.6-1.0 Ma)							Middle Irvingtonian (1.0-0.6 Ma)	Late Irvingtonian (0.6-0.3 Ma)	Early Ranchola-brean[1] (0.3Ma-130 ka)	Late Ranchola-brean[2] (130-10 ka)	Recent
Haile 16A	Leisey Shell Pit	Pool Branch	Payne Creek Mine	Crystal River	Rigby Shell Pit	Haile 21A	McLeod	Coleman 2A			
–	–	–	–	–	–	–	–	X	X	X	X
X	X	–	X	–	X	X	X	X	X	X	–
X	X	X	X	X	X	–	–	–	–	–	–
–	–	–	–	–	–	–	X	X	X	X	–
–	X	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	–
X	X	–	X	–	X	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
X	X	–	X	X	–	–	–	–	X	X	–
–	–	–	–	–	–	–	–	–	X	X	–
–	–	–	–	–	–	–	–	–	–	–	–
X	X	–	X	X	–	–	X	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	–
X	X	?	X	X	–	?	–	–	–	–	–
–	X	X	–	–	–	–	–	–	–	–	–
X	–	–	–	–	–	X	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	X	–
–	–	–	–	–	–	–	–	–	–	–	–
–	X	–	–	–	–	X	X	X	–	–	–
–	–	–	–	–	–	-	–	–	X	X	–
–	X	–	–	X	X	X	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	?	X
–	–	–	–	–	–	–	–	–	–	–	–
–	X	–	–	–	–	–	–	–	X	X	X
–	–	–	–	–	–	–	–	X	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	X	X	X	X
X	X	–	–	X	–	X	–	–	–	–	–
X	X	–	X	X	X	–	X	X	–	–	–
–	–	–	–	–	–	–	–	–	X	X	–
–	–	–	–	–	–	–	–	X	X	X	X[3]
–	–	–	–	–	–	–	–	–	–	X	–

Table 2 Continued.

	Late Blancan (2.5-2.0 Ma)					Earliest Irvingtonian (2.0-1.6 Ma)	
	Santa Fe River 1	Haile 15A	Macasphalt Shell Pit	Kissimmee River	Haile 7C	Inglis 1A	De Soto Shell Pit
Spilogale putorius	–	–	–	–	–	–	–
Spilogale sp.	–	–	–	–	–	X	–
Lutra canadensis	–	–	–	–	–	–	–
Satherium piscinarium	–	X	–	–	–	–	X
Trigonictis cookii	–	–	–	–	–	–	–
Trigonictis macrodon	–	–	X	–	–	X	X
Callophoca obscura	–	–	X	X	–	–	–
Monachus tropicalis	–	–	–	–	–	–	X
Dinobastis serus	–	–	–	–	–	–	–
Felis amnicola	–	–	–	–	–	–	–
Homotherium n. sp.	?	–	–	?	–	X	–
Lynx rufus	–	–	–	–	–	–	–
Lynx sp.	–	–	X	–	–	X	–
Miracinonyx inexpectatus	X	–	–	–	–	X	–
Miracinonyx cf. *M. trumani*	–	–	–	–	–	–	–
Panthera atrox	–	–	–	–	–	–	–
Panthera onca	–	–	–	–	–	–	–
Puma concolor	–	–	–	–	–	–	–
Smilodon fatalis	–	–	–	–	–	–	–
Smilodon gracilis	X	X	–	–	–	X	–
Chasmaporthetes ossifragus	X	–	–	–	–	X	X
Castor canadensis	–	X	–	–	–	–	–
Castoroides leiseyorum	–	–	–	–	–	–	–
Castoroides ohioensis	–	–	–	–	–	–	–
Geomys pinetis	–	–	–	–	–	–	–
Geomys propinetis	–	X	X	–	–	X	X
Thomomys orientalis	–	–	–	–	–	–	–
Zapus sp.	–	–	–	–	–	–	–
Erethizon dorsatum	–	–	–	–	–	–	–
Erethizon kleini	–	–	–	–	–	X	–
Erethizon sp.	–	–	–	–	X	–	–
Hydrochaeris holmesi	–	X	–	–	–	X	–
Neochoerus dichroplax	–	–	X	X	–	–	–
Neochoerus pinckneyi	–	–	–	–	–	–	–

Table 2 Extended/Continued.

			Late Early Irvingtonian (1.6-1.0 Ma)				Middle Irvingtonian (1.0-0.6 Ma)	Late Irvingtonian (0.6-0.3 Ma)	Early Rancholabrean (0.3Ma-130 ka)	Late Rancholabrean (130-10 ka)	Recent
Haile 16A	Leisey Shell Pit	Pool Branch	Payne Creek Mine	Crystal River	Rigby Shell Pit	Haile 21A	McLeod	Coleman 2A			
–	X	–	–	–	–	–	–	X	X	X	X
–	–	–	–	–	–	–	–	–	–	–	–
–	X	–	–	X	–	–	–	–	–	X	X
–	–	–	–	–	–	–	–	–	–	–	–
X	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	X	–	–	–	X	–	–	–	–	X	X[4]
–	–	–	–	–	–	–	–	–	–	X	–
–	–	–	–	–	–	–	–	–	–	X	–
X	X	–	–	–	–	X	–	–	–	–	–
X	X	–	–	–	–	X	–	X	X	X	X
–	–	–	–	–	–	–	–	–	–	–	–
–	X	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	X	–
–	–	–	–	–	–	–	–	–	–	X	–
–	–	–	–	–	–	–	X	X	X	X	X[3]
–	–	–	–	–	–	–	–	–	–	X	X
–	–	–	–	–	–	–	–	–	X	X	–
–	X	–	–	X	–	X	X	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	X	X
–	X	–	–	?	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	–
–	X	–	X	–	–	X	–	X	X	X	X
X	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	X	X	X	–
X	–	–	–	–	–	–	–	–	–	–	–
X	X	–	–	–	–	X	–	X	–	X	X[3]
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	X	X	X	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	–

Table 2 Continued.

	Late Blancan (2.5-2.0 Ma)					Earliest Irvingtonian (2.0-1.6 Ma)	
	Santa Fe River 1	Haile 15A	Macasphalt Shell Pit	Kissimmee River	Haile 7C	Inglis 1A	De Soto Shell Pit
Neochoerus sp.	–	–	–	–	–	–	–
Neotoma floridana	–	–	–	–	–	–	–
Neotoma sp.	–	–	–	–	X	X	–
Oryzomys palustris	–	–	–	–	–	–	–
Peromyscus large sp.	–	–	–	–	–	–	?
Podomys floridanus	–	–	–	–	–	–	–
Podomys n. sp.	–	–	–	–	–	–	–
Sigmodon bakeri	–	–	–	–	–	–	–
Sigmodon curtisi	–	–	–	–	–	X	X
Sigmodon hispidus	–	–	–	–	–	–	–
Sigmodon libitinus	–	–	–	–	–	–	–
Sigmodon medius	–	X	X	–	–	–	–
Sigmodon minor	–	–	–	–	–	–	X
Atopomys salvelinus	–	–	–	–	–	–	X
Microtus pennsylvanicus	–	–	–	–	–	–	–
Neofiber alleni	–	–	–	–	–	–	–
Neofiber leonardi	–	–	–	–	–	–	–
Ondatra annectens	–	–	–	–	–	–	–
Ondatra idahoensis	–	–	–	–	–	X	X
Ondatra zibethicus	–	–	–	–	–	–	–
Pitymys aratai	–	–	–	–	–	–	–
Pitymys hibbardi	–	–	–	–	–	–	–
Pitymys pinetorum	–	–	–	–	–	–	–
Pedomys n. sp.	–	–	–	–	–	–	–
Synaptomys australis	–	–	–	–	–	–	–
Synaptomys n. sp.	–	–	–	–	–	–	–
Lepus cf. *L. townsendii*	–	–	–	–	–	–	–
Lepus sp.	–	–	–	–	–	X	–
Sylvilagus floridanus	–	–	–	–	–	–	–
Sylvilagus palustris	–	–	–	–	–	–	–
Sylvilagus webbi	–	?	X	?	?	X	X
Mylohyus floridanus	X	X	X	–	–	–	–
Mylohyus fossilis	–	–	–	–	–	–	–
Platygonus bicalcaratus	X	–	X	X	–	–	–

Table 2 Extended/Continued.

			Late Early Irvingtonian (1.6-1.0 Ma)				Middle Irvingtonian (1.0-0.6 Ma)	Late Irvingtonian (0.6-0.3 Ma)	Early Rancholabrean (0.3Ma-130 ka)	Late Rancholabrean (130-10 ka)	Recent
Haile 16A	Leisey Shell Pit	Pool Branch	Payne Creek Mine	Crystal River	Rigby Shell Pit	Haile 21A	McLeod	Coleman 2A			
–	X	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	X
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	X
–	–	–	X	–	–	X	–	–	–	–	–
–	–	–	–	–	–	–	–	X	X	X	X
X	X	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	X	X	X	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	X
X	X	–	X	–	–	X	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
X	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–		–	–	–	X	X
–	–	–	–	–	–	–	–	X	X	X	X
–	–	–	–	–	–	–	X	–	–	–	–
–	X	X	X	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	X	X[3]
–	–	–	–	–	–	–	–	X	–	–	–
–	–	–	–	–	–	–	–	–	X	–	–
–	–	–	–	–	–	–	–	–	–	X	X
X	X	–	X	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	–
X	X	–	–	–	–	–	–	–	–	–	–
–	X	–	–	–	–	–	–	–	–	–	–
–	–	–	X	–	–	–	X	X	–	–	–
–	X	–	X	–	–	X	–	X	X	X	X
–	–	–	X	–	–	–	–	–	X	X	X
X	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
?	X	X	–	–	–	–	–	X	X	X	–
–	–	–	–	–	–	–	–	–	–	–	–

Table 2 Continued.

	Late Blancan (2.5-2.0 Ma)					Earliest Irvingtonian (2.0-1.6 Ma)	
	Santa Fe River 1	Haile 15A	Macasphalt Shell Pit	Kissimmee River	Haile 7C	Inglis 1A	De Soto Shell Pit
Platygonus compressus	–	–	–	–	–	–	–
Platygonus cumberlandensis	–	–	–	–	–	–	–
Platygonus vetus	–	–	–	–	–	X	–
Hemiauchenia blancoensis	X	–	X	–	–	–	–
Hemiauchenia macrocephala	–	X	–	?	–	X	X
Hemiauchenia n. sp.	–	–	–	–	–	X	X
Palaeolama mirifica	–	–	–	–	–	–	–
Capromeryx arizonensis	X	–	–	X	–	X	X
Odocoileus virginianus	X	X	X	X	X	X	X
Bison antiquus	–	–	–	–	–	–	–
Bison latifrons	–	–	–	–	–	–	–
Bovidae, gen. indet.[5]	–	–	X	–	–	X	–
Tapirus haysii	–	–	–	–	–	–	–
Tapirus veroensis	–	–	–	–	–	–	–
Tapirus n. sp.	?	?	–	?	X	X	X
Cormohipparion emsliei	–	X	X	–	–	–	–
Nannippus peninsulatus	X	X	X	X	–	–	–
Equus (Dolichohippus) sp.	X	X	X	X	–	–	–
Equus "fraternus"	–	–	–	–	–	–	–
Equus "leidyi"	–	–	–	–	–	X	X
Equus (Hemionus) n. sp.	–	–	–	–	–	–	–
Equus alaskae group	–	–	–	–	–	–	–
Equus laurentius group	–	–	–	–	–	–	–
Rhynchotherium praecursor	X	–	X	–	–	–	–
Cuvieronius tropicus	–	–	–	X	X	–	X
Mammut americanum	–	–	–	–	–	X	X
Mammuthus hayi	–	–	–	–	–	–	–
Mammuthus columbi	–	–	–	–	–	–	–

[1] The early Rancholabrean fauna is a composite list compiled from the following sites: Bradenton, Daytona Beach, Haile 7A, Haile 8A, Oldsmar, Williston 3A, and Williston 3B.

[2] The late Rancholabrean fauna is a composite list compiled from the following sites: Arredondo 2A, Cutler Hammock, Devils Den, Ichetucknee River, Melbourne, Monkey Jungle Hammock, Reddick 1, Seminole Field, and Vero.

Table 2 Extended/Continued.

Late Early Irvingtonian (1.6-1.0 Ma)							Middle Irvingtonian (1.0-0.6 Ma)	Late Irvingtonian (0.6-0.3 Ma)	Early Rancholabrean (0.3Ma-130 ka)	Late Rancholabrean (130-10 ka)	Recent
Haile 16A	Leisey Shell Pit	Pool Branch	Payne Creek Mine	Crystal River	Rigby Shell Pit	Haile 21A	McLeod	Coleman 2A			
–	–	–	–	–	–	–	–	–	X	X	–
–	–	–	–	–	–	–	–	X	X	–	–
?	X	X	–	–	–	X	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	X	X	X	X	X	–	–	X	X	X	–
–	–	–	–	–	–	–	–	–	–	–	–
X	X	–	X	–	–	X	X	X	X	X	–
–	–	–	–	–	–	–	–	–	–	–	–
–	X	X	X	X	X	X	X	X	X	X	X
–	–	–	–	–	–	–	–	–	–	X	–
–	–	–	–	–	–	–	–	–	X	–	–
–	–	–	–	–	–	–	–	–	–	–	–
X	X	X	X	X	–	X	X	–	–	–	–
–	–	–	–	–	–	–	–	X	X	X	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–
X	X	–	–	–	–	–	–	–	–	–	–
X	X	X	X	X	X	X	X	X	–	–	–
–	X	X	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	X	X	–
–	–	–	–	–	–	–	–	–	X	X	–
–	–	–	–	–	–	–	–	–	–	–	–
–	X	X	X	X	X	X	–	–	X	–	–
–	X	X	–	–	–	–	–	–	X	X	–
–	X	–	X	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	?	X	X	–

[3] No longer found in Florida, but still survives elsewhere in North America
[4] The Caribbean monk seal has gone extinct within the past 40 years.
[5] J. McDonald (pers. comm.) thinks this taxon may be related to Old World Pliocene *Bison*.

A quote from Lundelius et al. (1987:218) is particularly appropriate to the difficulties encountered when trying to correlate Florida Pliocene and Pleistocene faunas: "Latitudinal, regional, and ecological factors lead to faunal provincialism that together with lack of radiometric and paleomagnetic control makes correlation of faunas difficult." Because most Florida Blancan and Irvingtonian vertebrate faunas lack radiometric and paleomagnetic control, we must rely almost entirely on biochronologic comparisons with well-dated faunas from the western United States. However, these correlations may be limited by the faunal provincialism noted by Lundelius et al. (1987). For instance in eastern North America the late Blancan and early Irvingtonian (2.5 to 1.0 Ma) are represented almost exclusively by vertebrate faunas from Florida, many of which appear to sample a more tropical fauna than typical western faunas of this time period. Despite certain peculiarities in Florida Blancan and Irvingtonian faunas, there are still more similarities than differences between Florida and western faunas of this age, and these faunal similarities will be stressed throughout this paper.

Data on sea level are helpful in placing certain Florida vertebrate faunas in the context of glacial and interglacial stages. There are two general circumstances in which information derived from vertebrate fossil sites can provide some indication of sea level. Low sea level faunas, presumably deposited during glacial intervals, are indicated by sites collected below present sea level that contain no evidence of marine vertebrates. By these criteria, the late Blancan St. Petersburg Times LF and the early Irvingtonian Inglis 1A and Crystal River Power Plant local faunas are examples of low sea level faunas. High sea level faunas, presumably reflecting interglacial conditions, are indicated by sites collected well above modern sea level that contain marine vertebrates. Examples of high sea level faunas are the late Blancan Haile 15A and Kissimmee River sites, the early Irvingtonian De Soto Shell Pit, and the early Rancholabrean Daytona Beach and Oldsmar local faunas. The number of glacial and interglacial intervals, and hence the number of eustatic sea level changes throughout the late Pliocene and Pleistocene, appears to be much greater (Shackleton and Opdyke 1977) than the four glaciations (Nebraskan, Kansan, Illinoian, and Wisconsinan) traditionally recognized during the Pleistocene. We use the relative sea level position of several Florida vertebrate fossil sites, in conjunction with other geochronological data, to help determine the placement of the site relative to the worldwide sea level curve (e.g. Haq et al. 1987).

No Florida pre-Rancholabrean vertebrate faunas have been radioisotopically dated, although attempts are underway to obtain uranium-series dates on corals collected from nearshore marine shell beds in association with vertebrate faunas. However, uranium-series dates are not reliable for sites older than about one million years (Szabo 1985). Bender (1973) determined helium/uranium ages on samples of corals from several Florida Pliocene and Pleistocene marine geologic units, including the Pinecrest Beds and Caloosahatchee Formation. This dating

technique has not been applied recently, nor has it been used to directly date any vertebrate faunas. Other methods of radioisotopic dating (K/Ar, Ar/Ar, etc.) are not applicable in Florida sites because the surficial geology of this region is devoid of basalt flows, volcanic ash beds, or other igneous rocks containing minerals normally used for dating vertebrate-bearing beds in the western United States and elsewhere.

Long stratigraphic sequences with a paleomagnetic polarity reversal chronology are unknown from the Florida Plio-Pleistocene. However, paleomagnetic signatures (i.e. normal or reversed) have now been obtained from two Florida vertebrate faunas, including Leisey (Webb et al. 1989; MacFadden this volume) and the late Blancan Macasphalt (=APAC) Shell Pit (Jones et al. 1991). Most Blancan and Irvingtonian karst deposits in northern Florida (e.g. Haile 15A, Haile 16A, McLeod, Coleman 2A) were destroyed by mining operations many years ago, and thus are no longer available for paleomagnetic sampling. In the future, we intend to obtain a paleomagnetic signature for all Florida Blancan and Irvingtonian sites containing sediments suitable to this type of analysis.

An integrated approach has been used to determine the age of the vertebrate-bearing deposits at the Leisey Shell Pit, applying data from paleomagnetic polarity stratigraphy, strontium isotope chronology, relative sea level position, and mammalian and molluscan biochronology (see Jones 1992). Many Florida Plio-Pleistocene vertebrate sites, particularly deposits in the northern portion of the peninsula, do not lend themselves to this type of integrated analysis. The majority of northern Florida Blancan and Irvingtonian sites are composed of terrestrial or freshwater sediments that occur as isolated cave, sinkhole, or fissure fillings in Eocene marine limestones, and cannot be correlated to a regional stratigraphic sequence. Most also lack associated marine vertebrate and invertebrate faunas, thus eliminating the possibility of strontium isotope analysis, determination of relative sea level position, or comparison with marine molluscan biochronology. Therefore, sites such as the Leisey Shell Pit are extremely important cross-references that allow us to compare terrestrial and marine biochronologies, and to contrast these results with data obtained from other geochronological techniques.

Biochronology of the Leisey Mammalian Fauna.—The Leisey Shell Pit Local Fauna has one of the richest samples of large terrestrial mammals known from any Irvingtonian site in North America. Among the 49 mammalian taxa listed in Table 1, 33 are large mammals. Large herbivores numerically dominate the Leisey 1A mammalian fauna, in particular the llamas *Palaeolama mirifica* and *Hemiauchenia macrocephala*, two species of the horse *Equus*, the ground sloths *Paramylodon harlani* and *Nothrotheriops texanus*, the peccary *Platygonus vetus*, and the mammoth *Mammuthus hayi*. The most common large carnivore is the sabercat *Smilodon gracilis*. The small mammal fauna consists of one species of shrew, two lagomorphs, and nine rodents. Five marine mammals have been

identified from Leisey, including three odontocete cetaceans, the manatee *Trichechus*, and the seal *Monachus*.

The age of the Leisey Shell Pit LF has been determined principally from its land mammal fauna. However, the biochronologic significance of selected non-mammalian taxa from Leisey will also be discussed. The large and well preserved samples of carnivores, ungulates, and xenarthrans, and to a lesser extent rodents, from Leisey permit detailed taxonomic and biochronological comparisons of this fauna with well known Irvingtonian faunas from Florida and elsewhere in North America (e.g. Kurtén and Anderson 1980; Lundelius et al. 1987; Repenning 1987). Preliminary biostratigraphic analyses of the Leisey Shell Pit vertebrate fauna have already been published (Hulbert and Morgan 1989; Webb et al. 1989). These studies and the present analysis indicate that the Leisey Shell Pit LF correlates to the later half of the early Irvingtonian between 1.6 and 1.0 Ma, and most likely to the later half of this interval. This age assignment is based on a number of mammalian taxa, including first appearances of immigrants from both South America and the Old World, overlapping range zones of certain indicator species, the evolutionary stage of taxa within certain well known lineages, and the absence of most taxa characteristic of either Blancan or middle Irvingtonian and younger faunas.

In addition to age differences, there are many other reasons why taxa may be absent from a fauna, including collecting bias, taphonomic or paleocological factors, and differences in biogeography. The faunal differences between the four individual sites comprising the Leisey Shell Pit LF are probably related to paleoecological factors. For instance, at Leisey 1A *Mammuthus* is the dominant proboscidean and *Nothrotheriops* and *Paramylodon* are the only two ground sloths present, whereas the gomphothere *Cuvieronius* and the giant ground sloth *Eremotherium* are the most common members of these two groups in the Leisey Shell Pit 3 site. Other faunal anomalies between the Leisey sites, such as the presence of *Glyptotherium arizonae* only at the base of the lower shell bed in Leisey Pit 1, may reflect slight differences in age between the collecting localities.

Xenarthra.--Like many other Florida Pliocene and Pleistocene sites, the Leisey Shell Pit LF has a diverse sample of xenarthrans, including three genera of armadillos, one genus of glyptodont, and four genera of ground sloths. Among Leisey xenarthrans, only the armadillo *Dasypus bellus* and the ground sloth *Paramylodon harlani* are considered conspecific with Rancholabrean species. *D. bellus* first appears in Florida during the late Blancan and persists throughout the remainder of the Pliocene and Pleistocene, going extinct at the end of the Rancholabrean. Although *D. bellus* is the only species of *Dasypus* recognized in North America during this time period, this armadillo shows a substantial size increase during its 2.5 million year history (Robertson 1976). The Leisey sample

of *D. bellus* is intermediate in size between small specimens from the late Blancan and the more typical large Rancholabrean form (Downing and White this volume).

The taxonomic and evolutionary history of the giant armadillo or pampathere *Holmesina* has been reviewed by Edmund (1985, 1987) and Hulbert and Morgan (1993). These studies documented significant evolutionary change in *Holmesina* from its first appearance in North America in the late Blancan until its extinction in the late Rancholabrean. Hulbert and Morgan (1993) referred the Leisey sample to the smaller of the two recognized species, *H. floridanus*, rather than to the much larger *H. septentrionalis*, which occurs in the middle Irvingtonian through Rancholabrean. They divided Florida *Holmesina* samples into four recognizable groups that are useful in a biochronologic context: 1) very small individuals of *H. floridanus* are known only in late Blancan sites, such as the type locality Haile 15A; 2) a slightly larger form referred to *H. floridanus* occurs in the latest Blancan Haile 7C LF; 3) an intermediate-sized form also referred to *H. floridanus* is known from the early Irvingtonian; and 4) the very large species *H. septentrionalis* ranges from the middle Irvingtonian through the Rancholabrean. Intermediate-sized specimens of *H. floridanus*, such as those found at Leisey, help restrict the age of this fauna to early Irvingtonian (2.0 to 1.0 Ma). The oldest record of *Holmesina* outside of Florida is from the early Irvingtonian Gilliland LF in Texas (Hibbard and Dalquest 1966), an approximate temporal equivalent of Leisey.

One of the most intriguing members of the Leisey mammalian fauna is a new genus and species of large armadillo, *Pachyarmatherium leiseyi*, named and described by Downing and White (this volume). The presence of an undescribed shelled edentate from several Irvingtonian sites in southern Florida has been known for some time based on a small sample of osteoderms. This taxon had been confused with *Dasypus bellus* until the discovery of an extensive sample of small, but very thick, hexagonal osteoderms from the Leisey Shell Pit. *Pachyarmatherium leiseyi* also appears to be a useful biostratigraphic indicator within the state, as all records are either late Blancan or early Irvingtonian. The oldest known specimens of *P. leiseyi* are from the late Blancan Kissimmee River 6 Site and the earliest Irvingtonian Forsberg Shell Pit LF (late Pliocene). Late early Irvingtonian faunas such as Leisey and Payne Creek represent the youngest known occurrences of this species.

Glyptotherium has a rather spotty distribution in Florida, both geographically and chronologically. It is one of the earliest Neotropical immigrants to participate in the Great American Interchange, where it is first recorded from late Blancan faunas in Arizona, Texas, and peninsular Florida (Gillette and Ray 1981). Except for the Florida samples, Gillette and Ray (1981) referred all other North American Blancan glyptodonts to the small species *G. texanum*. They tentatively referred glyptodont osteoderms from the late Blancan Santa Fe River sites and the earliest Irvingtonian Inglis 1A LF to *G. arizonae*. *G. arizonae* is a large, thick-shelled species reported from three early Irvingtonian faunas in the western United States:

Curtis Ranch, Arizona (type locality); Holloman, Oklahoma; and Gilliland, Texas (Gillette and Ray 1981). Glyptodont fossils collected from late Blancan and early Irvingtonian sites in Florida (including Leisey) in the ten years since of the publication of Gillette and Ray's (1981) monograph all appear to be referable to *G. arizonae* as well. *Glyptotherium* is rare in the Leisey Shell Pit LF, and is absent from the two richest sites, Leisey 1A and 3A. *G. arizonae* is represented at Leisey by a series of associated osteoderms collected from the base of the lower shell bed in Pit 1 in association with *Mammuthus*. *Glyptotherium* apparently was absent in Florida during the middle and late Irvingtonian. The smaller, thinner-shelled species, *Glyptotherium floridanum*, is restricted to Rancholabrean faunas in Florida (Gillette and Ray 1981).

Four species of ground sloths have been identified from Leisey, an undescribed species of *Eremotherium* (De Iuliis and Cartelle in prep.), *Megalonyx wheatleyi*, *Nothrotheriops texanus*, and *Paramylodon harlani* (McDonald this volume). The new species of *Eremotherium* is distinguished from the Rancholabrean species, *E. mirabile*, by the presence of four well developed claws on the manus, as opposed to only two claws in the later species (Hulbert et al. 1989). With the exception of the bones of digits 1 and 2 of the manus (metacarpals, phalanges, and claws), the remaining elements of the skeleton are very similar in the two species. The new species of *Eremotherium* has so far been confidently identified from the latest Blancan Haile 7C LF and the early Irvingtonian De Soto Shell Pit, Inglis 1A, Haile 16A, Leisey Shell Pit, Crystal River Power Plant, and Payne Creek Mine local faunas. Other records of *Eremotherium* of similar age, but lacking the diagnostic skeletal elements of the manus, include the late Blancan Kissimmee River, Lehigh Acres, and Brighton Canal local faunas and the early Irvingtonian Pool Branch and Haile 21A local faunas. The *Eremotherium* remains from these five sites are tentatively referred to the new four-clawed form based on their similarity in age to confirmed records of this species. *Eremotherium* has been recorded from the base of the lower shell bed in Leisey Pit 1 and is fairly common in Leisey Pit 3, but is absent from Leisey 1A and 3A. The largest Florida sample of *E. mirabile* is from the early Rancholabrean Daytona Beach LF (Edmund et al. in prep.). *E. mirabile* was very rare in Florida during the late Rancholabrean.

McDonald (1977) reviewed the fossil history of *Megalonyx* in Florida. He identified a small, endemic Florida form of the typical Blancan species, *Megalonyx leptostomus*, from the late Blancan Santa Fe River 1 LF and the earliest Irvingtonian Inglis 1A LF. Additional specimens of this dwarf *M. leptostomus* have now been identified from the late Blancan Macasphalt Shell Pit, Kissimmee River, St. Petersburg Times, and Haile 7C faunas and the earliest Irvingtonian De Soto Shell Pit LF. *Megalonyx* has only recently been recorded from the Leisey Shell Pit LF based on a nearly complete skull from Leisey 3B. This genus is absent from Leisey 1A and 3A. The Leisey *Megalonyx* is distinctly larger than the

Florida material of *M. leptostomus* and is here tentatively referred to *M. wheatleyi*. According to McDonald (1977), *M. wheatleyi* is intermediate in size between the smaller Blancan and earliest Irvingtonian *M. leptostomus* and the larger late Pleistocene species *M. jeffersonii*. Other Florida localities for *M. wheatleyi* are the late early Irvingtonian Haile 16A, Payne Creek Mine, and Crystal River Power Plant local faunas and the middle Irvingtonian McLeod LF (McDonald 1977). *M. wheatleyi* appears to be restricted to the late early and middle Irvingtonian in Florida, whereas the larger *M. jeffersonii* does not appear until the Rancholabrean. Additional records of *M. wheatleyi* include early Irvingtonian faunas from Holloman, Oklahoma and Vallecito Creek, California and middle Irvingtonian faunas from Port Kennedy Cave, Pennsylvania (type locality), Cumberland Cave, Maryland, and Cudahy, Kansas (McDonald 1977).

Nothrotheriops is unknown in North America prior to the early Irvingtonian, and thus is apparently one of the last genera of South American immigrants to participate in the Great American Interchange. Irvingtonian specimens of *Nothrotheriops* are now regarded as a separate species, *N. texanus*, distinguished by its smaller size and more slender cranium from the better known Rancholabrean species, *N. shastensis* (see Akersten and McDonald 1991; McDonald this volume). The oldest well-dated records of *N. texanus* are from the early Irvingtonian Vallecito Creek LF, California, Gilliland LF, Texas, El Golfo LF, Sonora, Mexico, and Leisey Shell Pit and Pool Branch of Florida (Hibbard and Dalquest 1966; McDonald 1985, this volume). The *Nothrotheriops* sample from Leisey 1A is the largest Irvingtonian sample of this genus in North America (McDonald this volume).

"*Glossotherium*" *chapadmalense* is one of the first South American immigrants to reach North America following the formation of the Panamanian isthmus. Although the systematic relationships remain unresolved, it appears that the younger species *Paramylodon harlani* was derived from "*G.*" *chapadmalense* sometime during the late Blancan. These two species almost certainly belong in the same genus (McDonald this volume). "*G.*" *chapadmalense* is a small species represented by a partial skeleton from the late Blancan Haile 15A LF (Robertson 1976). Other late Blancan records of "*G.*" *chapadmalense* include the Santa Fe 1, Macasphalt Shell Pit, and Kissimmee River local faunas from Florida (Table 2), as well as Mt. Blanco, Texas (Dalquest 1975) and 111 Ranch, Arizona (Galusha et al. 1984). The oldest Florida record of the larger species, *P. harlani*, is from the earliest Irvingtonian Inglis 1A LF. *P. harlani* is found in Florida throughout the Irvingtonian and Rancholabrean. McDonald (this volume) demonstrates a gradual size increase in this species from the early Irvingtonian through the Rancholabrean.

Carnivora.--Berta (this volume) identified two species of large canids from the Leisey Shell Pit LF, *Canis edwardii* and *C. armbrusteri*. Both of these canids

are restricted to North American Irvingtonian faunas. However, prior to the discovery of Leisey, *C. edwardii* was known only from early Irvingtonian faunas, whereas *C. armbrusteri* was restricted to middle and late Irvingtonian faunas. These two species are now known to co-occur in two late early Irvingtonian sites in Florida, Leisey and Haile 21A. *C. edwardii* also is known from five other Florida early Irvingtonian faunas, including the earliest Irvingtonian Inglis 1A, De Soto Shell Pit and Forsberg Shell Pit local faunas and the late early Irvingtonian Crystal River Power Plant and Rigby Shell Pit local faunas. *C. armbrusteri* has also been identified from the late middle Irvingtonian McLeod Limerock Mine and the late Irvingtonian Coleman 2A LF (Martin 1974; Berta this volume). Florida records of *C. edwardii* and *C. armbrusteri* suggest that the overlapping range zone of these two species occurs only during a restricted interval of time in the late early Irvingtonian.

The sample of the sabercat *Smilodon gracilis* from Leisey is the most complete known from any Irvingtonian site (Berta this volume). Although the Leisey specimens are referable to *S. gracilis*, Berta (1987; this volume) noted that certain evolutionary changes occurred within this species during the early and middle Irvingtonian. *S. gracilis* is also well represented by material from the earliest Irvingtonian Inglis 1A LF and the middle Irvingtonian Port Kennedy Cave (type locality) and McLeod Limerock Mine local faunas (Berta 1987; this volume). The Leisey *S. gracilis* is intermediate in size and several morphological features between the samples from the older Inglis 1A LF and the younger Port Kennedy and McLeod sites (Berta 1987; this volume). There are no late Irvingtonian records of *Smilodon* from Florida. The larger and more advanced species, *S. fatalis* (=S. *populator* of Berta 1985), first occurs at this time elsewhere in North America (Berta 1987; Lundelius et al. 1987). *S. fatalis* appears in Florida during the early Rancholabrean and is found there throughout the remainder of the Pleistocene.

A large and possibly undescribed species of the machairodont cat *Homotherium* is represented at Leisey by a few isolated elements (Berta this volume). A partial skeleton of this species, including the skull and mandibles, is known from the correlative Haile 21A LF. Other fossils of this large *Homotherium* have been identified from Inglis 1A, Haile 16A, and possibly the late Blancan Santa Fe River 1 and Kissimmee River faunas. The large *Homotherium* present in Florida late Blancan and early Irvingtonian faunas is distinct from *Dinobastis serus* (see Berta this volume), a smaller sabercat known principally from the Rancholabrean, including the Reddick 1A LF in Marion County (Waldrop 1974).

The fossil record of the North American cheetah-like cat, *Miracinonyx inexpectatus*, has recently been reviewed (Van Valkenburgh et al. 1990). They reported *M. inexpectatus* from faunas of late Blancan through middle Irvingtonian age, including several specimens from Inglis 1A. Additional Florida records of *M.*

inexpectatus not listed by Van Valkenburgh et al. (1990) are from Leisey (Berta this volume) and the late Blancan Santa Fe River 2.

The large tremarctine bear, *Arctodus pristinus*, occurs in two late Blancan faunas and eight Irvingtonian faunas in Florida, including Leisey 1A (Emslie this volume). The oldest records of *A. pristinus* in Florida are isolated teeth from the late Blancan Kissimmee River and Santa Fe River 1 faunas. Because this species is found throughout the Irvingtonian in Florida (Table 2), its presence does not place a fauna more precisely within this NALMA. There appears to be a chronological separation of tremarctine bears in Florida; *Arctodus pristinus* is found in the late Blancan and Irvingtonian and the smaller *Tremarctos floridanus* is restricted to the Rancholabrean. This may apply only in Florida, as the large bear *Arctodus simus* is widely distributed in North America during the Rancholabrean and *T. floridanus* has been reported from several western Blancan and Irvingtonian sites (Kurtén and Anderson 1980).

The river otter *Lutra* is an old World immigrant that first arrived in North America during the Irvingtonian (Kurtén and Anderson 1980; Lundelius et al. 1987). The earliest previously reported North American records of *Lutra* are from the middle Irvingtonian Cumberland Cave and Port Kennedy Cave faunas (Kurtén and Anderson 1980). The oldest well documented record of *Lutra* in Florida, and possibly North America as well, is from the Leisey Shell Pit LF. A well preserved mandible from Leisey 3B is similar in size to extant *L. canadensis*, whereas two associated upper teeth of *Lutra* from Leisey 1A are distinctly larger than the modern species. A large extinct otter, *L. parvicuspis*, described from Cumberland Cave (Gidley and Gazin 1933), has been synonymized with *L. canadensis* by most recent authors (e.g. Kurtén and Anderson 1980; Berta this volume). *L. canadensis* has also been identified from the Crystal River Power Plant, a close faunal correlate of Leisey.

A large raccoon of the genus *Procyon* is present in many Florida late Blancan and Irvingtonian faunas, including Leisey (*Procyon* n. sp. in Table 2). Klein (1971) described the *Procyon* from Inglis 1A LF (listed as "*Procyon* n. sp." by Webb and Wilkins 1984) as intermediate in size and morphological features between the large species *P. rexroadensis* from the early Blancan Rexroad LF (Kurtén and Anderson 1980) and the living *P. lotor*. Morgan and Ridgway (1987) reported a large *Procyon* from the late Blancan St. Petersburg Times LF. A *Procyon* mandible from Leisey 1A tentatively referred to *P. lotor* (Berta this volume) is also larger than the modern raccoon and is probably the same as the Inglis species. The only Irvingtonian record of *Procyon* listed by Kurtén and Anderson (1980) was the small raccoon from Coleman 2A referred to *P. lotor* by Martin (1974).

Two genera of seals found in Florida late Pliocene and Pleistocene faunas, the monachine phocids *Monachus* and *Callophoca*, may provide some useful biochronological information. With the exception of a single bone of the recently

extinct Caribbean monk seal, *Monachus tropicalis*, from the late Rancholabrean Melbourne LF (Ray 1958), all other Florida records of *Monachus* are from the early Irvingtonian (Table 2). *Monachus* is known from two localities in the Caloosahatchee Formation of earliest Irvingtonian age, the De Soto Shell Pit LF and the Ortona Locks along the Caloosahatchee River, and two sites in the Bermont Formation of late early Irvingtonian age, Leisey Shell Pit and Rigby Shell Pit. The apparent absence of *Monachus* in Florida during the remainder of the Irvingtonian and most of the Rancholabrean may be an artifact of inadequate sampling of marginal marine faunas during this time interval. Monachine phocids also are present in four Florida late Blancan faunas, Brighton Canal, Kissimmee River, Macasphalt Shell Pit, and Richardson Road Shell Pit. These Blancan specimens appear to represent the large extinct genus, *Callophoca*, which also occurs in Florida early Pliocene (late Hemphillian) faunas from the Bone Valley Formation in central Florida (Morgan 1994).

Rodentia.--Martin (1969) reported several teeth of the giant beaver *Castoroides* from the presumed late Blancan Santa Fe River 1B LF. However, the mammalian fauna from Santa Fe 1B, like many of the Santa Fe faunas, consists of a mixture of late Blancan and Rancholabrean taxa (see more detailed discussion of Santa Fe sites below). Based on the absence of *Castoroides* from all other late Blancan and earliest Irvingtonian faunas in Florida, it is highly probable that the Santa Fe 1B giant beaver teeth are Rancholabrean in age. Removing this single Blancan record, *Castoroides* first appears in North America during the Irvingtonian. The oldest well-documented occurrences of *Castoroides* in Florida are from the late early Irvingtonian Leisey Shell Pit and Crystal River Power Plant local faunas. Specimens of *Castoroides* from Apollo Beach in Hillsborough County are probably early Irvingtonian in age as well, although this site contains a mixed assemblage of Irvingtonian and Rancholabrean taxa. Morgan and White (this volume) describe the Leisey *Castoroides* as a new species, *C. leiseyorum*. The more advanced species *Castoroides ohioensis* is common in Florida during the late Rancholabrean, particularly in faunas that sample freshwater depositional environments (Martin 1969).

Pocket gophers of the genus *Geomys* are first recorded in Florida from the late Blancan Haile 15A and Macasphalt Shell Pit local faunas. These late Blancan specimens were referred to *G. propinetis* by Morgan and Ridgway (1987), an extinct species originally described from the early Irvingtonian Inglis 1A and Haile 16A local faunas (Wilkins 1984). A small sample of pocket gopher teeth recently collected from the De Soto Shell Pit, a correlative of Inglis 1A, is here referred to *G. propinetis* as well (Table 2). The *Geomys* sample from the Leisey Shell Pit LF is intermediate in size between *G. propinetis* and the extant southeastern pocket gopher *G. pinetis*, but otherwise is very similar to the living species (Morgan and White this volume). Apparently, *G. pinetis* evolved in Florida during the early

Irvingtonian, presumably derived from *G. propinetis*. Specimens of *Geomys* from the late Irvingtonian Coleman 2A LF are indistinguishable from *G. pinetis* (Martin 1974; Wilkins 1984).

There are two caviomorph rodents in the Leisey Shell Pit LF, the capybara *Neochoerus* sp. and the porcupine *Erethizon dorsatum*. Both are Neotropical immigrants that reached North America in the late Blancan following the beginning of the Great American Interchange. Two described species of *Neochoerus* are known from Florida late Pliocene and Pleistocene faunas, *N. dichroplax* from the late Blancan (Ahearn and Lance 1980) and *N. pinckneyi* from the Rancholabrean (Ahearn 1981). Although the *Neochoerus* sample from Leisey lacks the diagnostic M3, the size and shape of the p4 differ from that of *N. pinckneyi*. More complete fossils are necessary to determine whether the Leisey *Neochoerus* is referable to *N. dichroplax* or represents a new species. The only Florida Blancan record of *Erethizon* is an associated palate and mandible from Haile 7C. Frazier (1981) described a small species, *E. kleini*, from Inglis 1A. Three well preserved porcupine mandibles from Leisey are much larger than *E. kleini*, and appear to be indistinguishable from the living species, *E. dorsatum*. *E. dorsatum* is also present in the early Irvingtonian Haile 16A and Apollo Beach local faunas and the late Irvingtonian Coleman 2A LF (Frazier 1981).

Martin (1979) reviewed the evolutionary history of the cotton rat *Sigmodon*. Six species of cotton rats are recorded from Florida late Pliocene and Pleistocene faunas. The small, primitive species, *S. medius*, occurs in two Florida late Blancan faunas, Haile 15A (Martin 1979) and Macasphalt Shell Pit (Morgan and Ridgway 1987). The similar species, *S. minor* (conspecific with *S. medius* according to Kurtén and Anderson 1980), is reported from eastern North America for the first time based on two teeth from the earliest Irvingtonian De Soto Shell Pit (Morgan and White this volume). The larger and more progressive species, *S. curtisi*, was recorded from the earliest Irvingtonian Inglis 1A LF by Martin (1979) and also occurs in the correlative De Soto Shell Pit LF (Morgan and White this volume). Martin (1979) described *S. libitinus* from the late early Irvingtonian Haile 16A LF. Morgan and White (this volume) report *S. libitinus* from the Leisey Shell Pit LF and two other correlative late early Irvingtonian faunas, Payne Creek Mine and Haile 21A. *S. libitinus* is intermediate in certain morphological features between *S. curtisi* from the earliest Irvingtonian and *S. bakeri* from the late Irvingtonian Coleman 2A LF (type locality) and several early Rancholabrean faunas (Martin 1979). The extant cotton rat *S. hispidus* is the typical species found in Florida late Rancholabrean faunas, although it first appears in the early Rancholabrean Daytona Beach and Haile 8A local faunas.

The oldest arvicoline rodent known from Florida is the primitive muskrat, *Ondatra idahoensis*, from the earliest Irvingtonian Inglis 1A and De Soto Shell Pit local faunas. *O. idahoensis* occurs in western faunas of similar age, such as Curtis Ranch in Arizona (Repenning 1987), as well as slightly older late Blancan faunas

(Blancan V of Repenning 1987), including Borchers, Kansas and Grand View, Idaho (the type locality). The larger and more advanced muskrat, *O. annectens*, is present at Leisey Shell Pit, as well as in the correlative Pool Branch and Payne Creek Mine local faunas from the Bone Valley Region in Polk County. *O. annectens* is a rather long-ranging species characteristic of late early and middle Irvingtonian faunas (Nelson and Semken 1970; Martin and Tedesco 1976; Repenning 1987). Western early Irvingtonian faunas containing *O. annectens* include Java, South Dakota (Martin and Tedesco 1976; Martin 1989), Kentuck and Wathena, Kansas (Repenning 1987) and Sappa, Nebraska (Martin and Schultz 1985).

Two other genera of arvicolines are recorded from Leisey, the bog lemming *Synaptomys* and the vole *Pedomys*. About ten complete arvicoline teeth from Leisey are referred to *Pedomys* by Morgan and White (this volume). The Leisey *Pedomys* are very similar to a large series of jaws and teeth from the slightly older Haile 16A LF currently being described as a new species by Robert Martin (in prep.). A third sample of this same species occurs in the correlative Payne Creek Mine LF (see discussion below). Two teeth from Leisey are referable to *Synaptomys* sp. A similar sample of *Synaptomys* from Haile 16A also is currently under study by Robert Martin. The Leisey and Haile 16A *Synaptomys* appear to be related to *S. australis*, a large, extinct species present in Florida Rancholabrean faunas (Martin, pers. comm.).

Perissodactyla.--Hulbert (this volume) describes the Leisey sample of the giant tapir, *Tapirus haysii*, and discusses the biochronology of the genus in Florida. A smaller, undescribed species of *Tapirus* is present in the earliest Irvingtonian Inglis 1A and De Soto Shell Pit local faunas, the latest Blancan Haile 7C LF, and possibly several other late Blancan sites as well (Table 2). *T. haysii* is known from the Blancan and Irvingtonian in the western United States, but this species has a more restricted range in Florida where it has been identified from ten late early or middle Irvingtonian sites (Hulbert this volume). The tapir from the late Irvingtonian Coleman 2A LF, although represented only by postcranial elements, is within the size range of *T. veroensis*, the common Florida Rancholabrean species.

The three species of *Equus* recognized in the Leisey Shell Pit LF (Hulbert, this volume) are of limited biochronologic use because of the chaotic state of the taxonomy of North American *Equus*. None of the Leisey *Equus* are definitely conspecific with named species in well-dated western faunas. The absence of the hipparionine horses *Nannippus* and *Cormohipparion*, found in Florida Blancan faunas, is suggestive of a post-Blancan age for Leisey. The most common horse at Leisey, *Equus "leidyi,"* occurs throughout the Irvingtonian in Florida. *E. "leidyi"* is very similar to, and possibly represents a small eastern subspecies of, *E. scotti*, a common late Blancan to early Rancholabrean species with a wide distribution in

western North American (Winans 1989). The second most common horse at Leisey is an apparently undescribed form of the subgenus *Hemionus*. This subgenus is first known from the late Blancan of western North America (Skinner 1972), where it persisted through the Rancholabrean (*E. francisci*, Lundelius and Stevens 1970; Winans 1989). Other than Leisey, this new species is provisionally identified based on limited samples of isolated teeth from Pool Branch, Apollo Beach, and Flamingo Waterway in Charlotte County. The rarest of the Leisey horses is *E. "fraternus"* which is much better represented at Haile 16A. Both the relationships and biochronological signficance of this species are poorly known.

Artiodactyla.--Two species of peccaries occur in the Leisey Shell Pit LF, *Mylohyus fossilis* and *Platygonus vetus*. In his review of the Leisey tayassuids, Wright (this volume) refers the sample of *Mylohyus* to *M. fossilis*, a species typical of middle Irvingtonian through late Rancholabrean faunas in the eastern and central United States. Kinsey (1974) described the small Blancan species *M. floridanus* from the late Blancan Haile 15A LF. *M. floridanus* has since been reported from the late Blancan Macasphalt Shell Pit as well (Morgan and Ridgway 1987). The Leisey *Mylohyus* is larger than other specimens of late Blancan or Rancholabrean *Mylohyus* examined from Florida.

Wright (this volume) notes that it is difficult to separate the various Blancan and Irvingtonian species of *Platygonus*, most of which are larger than the common Rancholabrean species, *P. compressus*. Large specimens of *Platygonus* from Florida late Blancan faunas (Table 2) generally have been referred to *P. bicalcaratus* (Webb 1974a; Morgan and Ridgway 1987). Wright (this volume) provisionally refers the Leisey *Platygonus* to *P. vetus*, a large species known from many early and middle Irvingtonian faunas, including large samples from Inglis 1A and Haile 21A. An even larger *Platygonus* from the late Irvingtonian Coleman 2A LF and the early Rancholabrean Haile 7A LF is tentatively referred to *P. cumberlandensis* (Martin 1974; Wright this volume). The smaller species, *P. compressus*, appears in Florida during the early Rancholabrean.

Camels are the most abundant large mammals in the Leisey Shell Pit LF, approached in numbers of individuals only by horses. Two camels have been identified from Leisey, *Palaeolama mirifica* and *Hemiauchenia macrocephala* (Webb and Stehli this volume; they use the species name *H. seymourensis* for the Leisey sample of this genus). *H. macrocephala* is a long-ranging species that first appeared in the late Blancan and survived until the end of the Pleistocene (Webb 1974b). A larger species, *H. blancoensis*, has been identified from several Florida late Blancan sites (Table 2; Webb 1974b; Morgan and Ridgway 1987). The occurrence of *Palaeolama* at Leisey represents one of the earliest North American records of the genus; only the sample from Haile 16A is older. The two major Leisey sites, Leisey 1A and 3A, differ significantly in their camel faunas. *Palaeolama* is the most abundant large mammal at Leisey 1A, outnumbering

Hemiauchenia by more than two to one. In contrast, *Hemiauchenia* overwhelmingly dominates the large vertebrate fauna at Leisey 3A and *Palaeolama* is absent.

Proboscidea.--The Leisey 1A proboscidean sample is predominantly composed of the mammoth *Mammuthus*, with only a few, mostly juvenile, individuals of the mastodon *Mammut americanum* and several fragmentary cheekteeth and tusks of the gomphothere *Cuvieronius tropicus* (see Webb and Dudley this volume). Leisey 3A is almost devoid of proboscideans, whereas *Cuvieronius* is the most common proboscidean in Leisey Shell Pit 3. The presence of *Cuvieronius* in Florida faunas was once thought to indicate an early Irvingtonian or older age (Brooks 1968). However, subsequent discoveries confirm that *Cuvieronius* occurs in Florida from the late Blancan throughout the Irvingtonian and into the early Rancholabrean. Although *Cuvieronius* is probably the most ubiquitous proboscidean in Florida Irvingtonian faunas, most of the fossils consist of isolated and/or fragmentary remains. The only comparatively rich samples of this genus from Florida are in the early Irvingtonian Punta Gorda LF, Charlotte County (Brooks 1968; Webb 1974a; see discussion below) and the early Rancholabrean Daytona Beach LF (Edmund et al. in prep.). The Daytona Beach site is the youngest recorded Florida occurrence of *Cuvieronius*.

Leisey Shell Pit 1A has one of the richest known Irvingtonian samples of *Mammuthus* (see Webb and Dudley this volume). The Leisey mammoth teeth are intermediate in morphological features between teeth of *M. meridionalis* and *M. imperator* as defined by Maglio (1973). Webb and Dudley restrict *M. meridionalis* to Old World mammoths and refer primitive North American mammoths from the early Irvingtonian to *M. hayi*. Webb (1974a) and Webb and Dudley (this volume) also discuss a sample of *M. hayi* from the Punta Gorda LF which is very similar to the Leisey *Mammuthus*. The late early Irvingtonian *Mammuthus* from Leisey and Punta Gorda are comparable to samples from the Gilliland LF in Texas and the Holloman LF in Oklahoma, and may be among the earliest mammoths in the New World. The next youngest Florida fauna containing a measurable sample of mammoths is the early Rancholabrean Bradenton LF. All Florida Rancholabrean specimens of *Mammuthus* are referable to the widespread species, *M. columbi*.

Sirenia and Cetacea.– The Sirenia and Cetacea are the only groups of Leisey mammals not covered in the individual taxonomic papers. The Leisey Shell Pit LF represents the earliest well documented North American record of the manatee *Trichechus*. Specimens of *Trichechus* from Leisey 1A consist of a partial skull cap (UF 87226), an isolated tooth (UF 87227), and the proximal humerus of a juvenile (UF 81514). Manatee fossils are more common at Leisey 3 and include a nearly complete skull in the National Museum of Natural History, a partial skull (UF 124557), a complete humerus (UF 135693), and a metacarpal (UF 129092).

Domning (1982) reported several supposed late Blancan manatee specimens from Santa Fe 1B, and noted that they were very similar to the living species *T. manatus*. Subsequent study of the Santa Fe 1B fauna (Morgan and Ridgway 1987 and discussion below) has shown that this site contains a mixture of late Blancan and Rancholabrean taxa. The abundance of manatee fossils in other Rancholabrean sites along the Santa Fe River suggests that the Santa Fe *Trichechus* is late Pleistocene as well. The Leisey *Trichechus* sample is currently under study by Daryl Domning.

Cetaceans are rare at Leisey. Two isolated teeth of small delphinids from Leisey 1A are tentatively identified as *Stenella* (UF 84919) and *Tursiops* (UF 84629). Three associated vertebrae (UF 142239) from Leisey 3B represent a much larger delphinid similar in size to the pilot whale *Globicephala*.

Biochronology of the Leisey Lower Vertebrate Fauna.– There are several taxa of lower vertebrates from the Leisey Shell Pit LF, including sharks, turtles, and birds, that provide some information relating to the age of the site. There is no established biochronology for any of these groups, and thus the age data are not so precise as those provided by the better known mammals. Furthermore, several of these taxa are restricted to Florida sites.

Shark teeth are common in certain units within the late Pliocene and Pleistocene shell bed sequence of central and southern Florida, but very little has been published previously on Florida sharks of this age (Scudder et al. this volume). In his review of Florida fossil sharks, Tessman (1969) did not mention any specimens younger than samples from the early Pliocene portion of the Bone Valley Formation.

Three extinct species of sharks, *Ginglymostoma serra*, *Isurus hastalis*, and *Hemipristis serra*, and the extinct ray *Rhynchobatus* sp. have been identified from the Leisey Shell Pit (Scudder et al. this volume). There are no published records of these species from other Florida Pleistocene faunas. All three of the sharks are known from the early Pliocene Bone Valley Formation (Tessman 1969), and *I. hastalis* and *H. serra* have been reported from the Pliocene Tamiami Formation (Morgan and Pratt 1983). It is possible that the teeth of the extinct species of sharks and rays were reworked into the early Pleistocene Bermont Formation in the Leisey Shell Pit from underlying Miocene sediments. Most of the Miocene shark teeth from Leisey are waterworn and have a different color of preservation, whereas two *H. serra* teeth from Leisey 1A and one from Leisey 3B were collected *in situ*, are in excellent condition, and have the same state of preservation as the remainder of the shark teeth from this unit.

The two teeth of *Isurus hastalis* from Leisey are broken and waterworn, and thus reworking from the underlying Miocene beds is a distinct possibility. A tooth of the extant shortfin mako shark, *I. oxyrinchus*, from the Leisey Shell Pit fauna apparently represents the first published fossil record of this species in Florida

(Tessman 1969). The age of the *Ginglymostoma serra* teeth from Leisey is uncertain owing to the rarity of this species in Florida fossil sites, although the specimens are not obviously reworked. Other Florida records of *G. serra* are from the Miocene and Pliocene (Tessman 1969). As is the case with the mako sharks, a living species of nurse shark, *G. cirratum*, occurs in the Leisey fauna as well.

Teeth of the living great white shark, *Carcharodon carcharias*, are relatively common at Leisey. This shark also has been identified from two late Pliocene sites in the Pinecrest Beds, the Macasphalt Shell Pit LF in Sarasota County (Waldrop and Wilson 1990) and the Kissimmee River LF, and from the earliest Irvingtonian Caloosahatchee Formation at the Cochran Shell Pit in Hendry County (Scudder et al. this volume). The oldest published record of *C. carcharias* in Florida is from the Bone Valley Formation of early Pliocene age (Tessman 1969). The extinct giant white shark, *C. megalodon*, was common and widespread in Florida during the late Miocene and early Pliocene.

The most abundant bony fish in the Leisey Shell Pit LF is the alligator gar, *Atractosteus spatula*, a species no longer found in the Florida peninsula (see Scudder et al. this volume). The closest living population of *A. spatula* is in the Florida panhandle (Wiley 1976). Despite its current absence from southern Florida, *A. spatula* is common in many Pliocene and early Pleistocene vertebrate sites in the southern half of the state. The youngest record of *A. spatula* from peninsular Florida is the early Rancholabrean Oldsmar LF in Pinellas County (Scudder et al. this volume).

Three turtles from Leisey provide some evidence for the age of the site. Auffenberg (1988) described a new species of small land tortoise, *Geochelone mlynarskii*, from the late Irvingtonian Coleman 2A LF. Meylan (this volume) refers the dwarf land tortoise from Leisey to this species, although he transfers it to the genus *Hesperotestudo*. Auffenberg (1988) noted that among members of the lineage of small land tortoises in Florida, termed the *incisa* group from the Rancholabrean species *H. incisa*, the major evolutionary changes occurred between the Blancan and early Irvingtonian, and between the late Irvingtonian and Rancholabrean. The Leisey sample is most similar morphologically to the Irvingtonian members of the *incisa* group, tentatively referred to *H. mlynarskii* (Auffenberg 1988; Meylan this volume).

The most common freshwater turtle in the Leisey Shell Pit LF is *Trachemys scripta*, an extant species now absent from central and southern peninsular Florida (Meylan this volume). Leisey represents one of the earliest records of *T. scripta*. Specimens from the earliest Irvingtonian Inglis 1A and De Soto Shell Pit faunas appear to be referable to the larger extinct species, *T. platymarginata* (synonymized with *T. idahoensis* by Jackson 1988). *T. platymarginata* originally was described from the late Blancan Haile 15A and Sante Fe River 1 faunas (Weaver and Robertson 1967), and is now known from several late Blancan faunas in the southern half of the state.

Meylan (this volume) documents the widespread occurrence of the alligator snapping turtle, *Macroclemys temmincki*, outside of its modern range during the late Pliocene and Pleistocene. *M. temmincki* is not currently found south of the Suwannee River in northern peninsular Florida. Fossil alligator snapping turtles are known from the late Hemphillian Palmetto Fauna, the late Blancan Macasphalt Shell Pit and St. Petersburg Times faunas, and the earliest Irvingtonian De Soto Shell Pit LF, as well as Leisey (Meylan this volume). The youngest fauna from southern Florida containing *M. temmincki* is the early Rancholabrean Oldsmar LF.

Several species of birds from Leisey are biochronologically useful (Emslie this volume). The small extinct loon, *Gavia concinna*, was previously known in Florida only from the late Hemphillian Bone Valley Formation in central Florida. Emslie (this volume) identifies *G. concinna* from Leisey thereby extending the biostratigraphic range of this species in Florida by about 3 million years. Leisey is the type locality for the extinct condor, *Gymnogyps kofordi* (Emslie 1988). This species is also known from the early Irvingtonian Haile 16A LF. Earlier records for the genus *Gymnogyps* include the late Blancan Macasphalt Shell Pit LF and the earliest Irvingtonian Inglis 1A LF (Emslie 1988; 1992a). All other fossils of *Gymnogyps* from Florida and elsewhere in North America are Rancholabrean in age and are referable to the living species *G. californianus* (Emslie 1988).

Emslie (this volume) refers a small sample of fossil turkeys from Leisey to *Meleagris leopoldi/M. anza*, following the usage of Steadman (1980). The Leisey *Meleagris* is similar to the large sample from Inglis 1A referred to *M. leopoldi/M. anza* by Steadman (1980). The Inglis and Leisey turkeys are smaller than specimens of *Meleagris* from Coleman 2A, a sample recognized by Steadman (1980) as intermediate between the Inglis turkeys and Rancholabrean specimens of the living species *M. gallopavo*.

Summary of Leisey Vertebrate Biochronology.– Knowledge of Florida Irvingtonian faunas has vastly increased over the past two decades to the point where Florida may be the most densely sampled geographic region in North America for the Irvingtonian Land Mammal Age. Owing to the lack of absolute dates, there is still a degree of uncertainty in correlating Florida Irvingtonian faunas within the state. Paleoecological and biogeographical factors magnify this uncertainty when Florida sites are compared to Irvingtonian faunas elsewhere in the United States. Despite these problems, the correlation of Florida Irvingtonian faunas both within and outside the state should be accurate within approximately 0.2 Ma.

Four of the genera used by Lundelius et al. (1987) to define the Irvingtonian NALMA occur in the Leisey Shell Pit LF, including *Smilodon*, *Lepus*, *Equus* s.s., and *Mammuthus*. Other genera identified from Leisey that have their first appearance in the Irvingtonian are *Nothrotheriops*, *Castoroides*, *Lutra*, and *Palaeolama*. Among the Irvingtonian immigrant genera recorded from Leisey,

Mammuthus and *Lutra* are Old World in origin and *Nothrotheriops* is Neotropical. *Smilodon*, *Castoroides*, and *Palaeolama* evolved in North America, but nonetheless are important biostratigraphic indicators. Irvingtonian faunas also are recognized by the absence of characteristic Blancan genera such as *Borophagus*, *Nannippus*, *Equus* (*Dolichohippus*), and *Rhynchotherium*. All of these genera are known from Florida late Blancan faunas (Morgan and Ridgway 1987), but are absent from Leisey.

The Leisey Shell Pit LF is younger than the earliest Irvingtonian Inglis 1A and De Soto Shell Pit local faunas (Table 2; Klein 1971; Webb 1974a; Webb and Wilkins 1984) based on the presence of *Mammuthus* and the absence of various Blancan holdover species found in the two older faunas, including the dwarf Florida form of *Megalonyx leptostomus*, *Chasmaporthetes ossifragus*, *Trigonictis macrodon*, and *Capromeryx arizonensis*. Furthermore, Leisey records the first occurrence in Florida of at least five genera not presently known from earliest Irvingtonian faunas: *Nothrotheriops*, *Lutra*, *Castoroides*, *Palaeolama*, and *Mammuthus*. There are also four genera of rodents present at Leisey that differ at the species level from their congeners at Inglis and/or De Soto (in parentheses), including *Geomys pinetis* (*G. propinetis*), *Erethizon dorsatum* (*E. kleini*), *Sigmodon libitinus* (*S. curtisi*), and *Ondatra annectens* (*O. idahoensis*).

Leisey is considerably older than the only other thoroughly studied Irvingtonian fauna from Florida, the late Irvingtonian Coleman 2A LF (Martin 1974). Leisey and Coleman share only a few diagnostic mammalian taxa, as the latter site actually more closely resembles early Rancholabrean faunas. Examples of typically Rancholabrean species at Coleman are *Didelphis virginiana*, *Holmesina septentrionalis*, *Neofiber alleni*, and *Tapirus veroensis*. Leisey lacks *Didelphis* and *Neofiber* and has the older species, *H. floridanus* and *T. haysii*. There are also two genera of rodents from Leisey that differ at the species level from their congeners or closely related genera at Coleman (in parentheses), *Sigmodon libitinus* (*S. bakeri*) and *Pedomys* n. sp. (*Pitymys aratai*). Leisey and Coleman do share several long-ranging Irvingtonian species, including *Canis armbrusteri*, *Arctodus pristinus*, and *Equus "leidyi."*

A more precise age refinement for Leisey is now possible based on comparisons with other Irvingtonian faunas from Florida, most of which were discovered during the past 20 years. Like Leisey, most of these faunas are younger than Inglis 1A and older than Coleman 2A. These intermediate Irvingtonian faunas include Haile 16A, Pool Branch, Payne Creek Mine, Crystal River Power Plant, Rigby Shell Pit, Haile 21A, and McLeod Limerock Mine (see Table 2 and discussions of the individual faunas below). All of these faunas except McLeod appear to be late early Irvingtonian in age, and therefore are roughly correlative with Leisey and between 1.6 and 1.0 Ma. McLeod is somewhat younger that the other faunas, probably late middle Irvingtonian in age (between 0.8 and 0.6 Ma).

The presence of three species at Leisey that are restricted to the late Blancan and/or early Irvingtonian serves to further constrain the age of this fauna, effectively ruling out a middle Irvingtonian age. The large glyptodont *Glyptotherium arizonae* occurs only in early Irvingtonian faunas in the western United States (Gillette and Ray 1981). In Florida, *G. arizonae* has been recorded from the earliest Irvingtonian Inglis and De Soto sites, as well as five late Blancan localities (Table 2). Leisey is the youngest Florida record of *G. arizonae*, and the only fauna in which this glyptodont has been found in association with *Mammuthus*. All occurrences of *Pachyarmatherium leiseyi* (Downing and White this volume) are from late Blancan and early Irvingtonian sites. *Canis edwardii* has been reported only from early Irvingtonian faunas (Kurtén and Anderson 1980). Florida specimens of this canid are known from both the earliest Irvingtonian (Inglis and De Soto) and the late early Irvingtonian (Leisey, Crystal River, Rigby, and Haile 21A).

At least three species of mammals found at Leisey appear to be restricted to late early Irvingtonian faunas in Florida. The cotton rat *Sigmodon libitinus* is known only from Leisey, Payne Creek, and the type locality Haile 16A LF (Martin 1979), all of which are late early Irvingtonian. These three faunas also share the same undescribed species of *Pedomys* (Martin in prep.). Although identified from only two Florida vertebrate faunas, Leisey and Pool Branch, *Nothrotheriops texanus* also appears to be restricted to the late early Irvingtonian. Elsewhere in North America, the biochronologic ranges of the canids *Canis edwardii* and *C. armbusteri* do not overlap, with the former restricted to the early Irvingtonian and the latter found in the middle and late Irvingtonian. Their co-occurrence at Leisey and Haile 21A confirms that *C. armbrusteri* first appears in the early Irvingtonian, at least in Florida.

Megalonyx wheatleyi is typically a middle Irvingtonian species, including the Florida sample from McLeod (McDonald 1977). However, a skull and other specimens from Leisey appear to be referable to *M. wheatleyi*, rather than to the smaller Florida form of *M. leptostomus*, typical of late Blancan and earliest Irvingtonian faunas. Leisey, Payne Creek, and Pool Branch all have the extinct muskrat, *Ondatra annectens*, a species found in late early and middle Irvingtonian faunas in the western United States. The large tapir, *Tapirus haysii*, also occurs only in the late early and middle Irvingtonian in Florida (Hulbert this volume). Analysis of several evolutionary lineages, in particular *Smilodon* and *Holmesina*, helps to clarify the age of Leisey. The Leisey representatives of these lineages further strengthen evidence from other taxa that this site best fits in the latter half of the early Irvingtonian, between 1.6 and 1.0 Ma.

Comparisons with Irvingtonian faunas in western North America indicate that Leisey is most similar in age to the Gilliland (Hibbard and Dalquest 1966) and Rock Creek (Troxell 1915) local faunas from Texas, the Holloman LF from

Table 3. List of mammals shared by three correlative late early Irvingtonian local faunas: Leisey Shell Pit, Florida; Gilliland, Texas; and Holloman, Oklahoma. Only species that occur at Leisey and one of the two other faunas are listed here. For complete mammalian faunal lists from these sites see Table 1 for Leisey, Hibbard and Dalquest (1966) for Gilliland, and Dalquest (1977) for Holloman.

Species	Leisey	Gilliland	Holloman
Xenarthra			
Holmesina floridanus	X	X	–
Glyptotherium arizonae	X	X	X
Paramylodon harlani	X	X	X
Nothrotheriops texanus	X	X	–
Carnivora			
Canis edwardii	X	X	–
Procyon sp.	X	X	–
Homotherium sp.	X	X	–
Lagomorpha			
Sylvilagus floridanus	X	X	–
Perissodactyla			
Tapirus haysii	X	X	X
Equus scotti or *E. "leidyi"*[1]	X	X	X
Equus (*Hemionus*) sp.	X	X	X
Artiodactyla			
Platygonus vetus	X	X	X
Hemiauchenia macrocephala	X	–	X
Odocoileus sp.	X	X	X
Proboscidea			
Cuvieronius tropicus	X	X	–
Mammuthus cf. *M. hayi*	X	X	X

[1] *Equus "leidyi"* is morphologically similar to *E. scotti* and possibly represents a smaller eastern subspecies of that species (Hulbert this volume).

Oklahoma (Dalquest 1977), the Kentuck, Nash, and Wathena local faunas from Kansas, the Sappa LF of Nebraska (Martin and Schultz 1985; Lundelius et al. 1987), and the Java LF from South Dakota (Martin 1973 1989). Sappa is the type fauna for the early Irvingtonian Sappan Subage (Schultz et al. 1978; Martin and Schultz 1985; Lundelius et al. 1987). Sappa, Java, and the three Kansas faunas mostly consist of small mammals, and thus correlation with Leisey is based either on absolute ages or comparisons with other faunas of similar age that have both large and small mammals.

Among the sites listed above, Leisey has the most taxa in common with Gilliland and Holloman (Table 3). All three faunas record the association of the

glyptodont *Glyptotherium arizonae* (Gillette and Ray 1981) and a primitive *Mammuthus* (Hibbard and Dalquest 1966; Dalquest 1977; Webb and Dudley this volume). These probably represent some of the earliest records of mammoths in North America, whereas *G. arizonae* is unknown in younger middle Irvingtonian faunas. The concurrent range zone of *Glyptotherium arizonae* and *Mammuthus* cf. *M. hayi* seems to occur only during a rather narrow interval of time in the late early Irvingtonian. Another age-diagnostic large mammal shared by these three faunas is the giant tapir, *Tapirus haysii*, a species restricted to late early and middle Irvingtonian faunas in Florida (Hulbert this volume). Leisey and Gilliland share several additional mammals that are found primarily in early Irvingtonian faunas, including the rare ground sloth, *Nothrotheriops texanus*, a medium-sized representative of the pampathere *Holmesina floridanus*, and the canid *Canis edwardii*. Hibbard and Dalquest (1966) stated that the Gilliland LF was post-Blancan and pre-Cudahy in age, or in other words, early Irvingtonian as defined here and by Lundelius et al. (1987). Although Dalquest (1977) regarded Gilliland and Holloman as earliest Irvingtonian in age, the presence of *Mammuthus* indicates that these two faunas are younger than faunas such as Curtis Ranch now generally regarded as earliest Irvingtonian (Lundelius et al. 1987).

Leisey and the correlative faunas mentioned above all are considered to be late early Irvingtonian in age (between 1.6 and 1.0 Ma). These faunas are somewhat younger than earliest Irvingtonian faunas (2.0 to 1.6 Ma) including: Curtis Ranch, Arizona; Inglis 1A; and De Soto Shell Pit. Leisey is older than typical North American middle Irvingtonian (=Cudahyan) faunas (1.0 to 0.6 Ma) including: the type Irvington fauna from California; Cudahy, Kansas; Conard Fissure, Arkansas; Vera, Texas; Cumberland Cave, Maryland; Port Kennedy Cave, Pennsylvania; and Hamilton Cave, West Virginia.

BIOCHRONOLOGY OF FLORIDA LATE PLIOCENE AND PLEISTOCENE VERTEBRATE FAUNAS

In the following section we present synopses of the most important Blancan and Irvingtonian vertebrate fossil sites from Florida, with the exception of Leisey which is discussed in detail above. Each synopsis includes a brief description of the location and physical setting of the site, discussion of the key mammalian taxa, reference to other factors such as relative sea level position that pertain to its age, and citations to the most important published references. Figure 4 is a map of Florida showing the location of the Blancan and Irvingtonian vertebrate faunas discussed in the text. More complete information on these sites is available in the locality files of the UF Vertebrate Paleontology Collections. Following these synopses we present a brief review of the Rancholabrean NALMA in Florida.

Table 2 is a list of 128 species of biochronologically diagnostic mammals from the most important Florida late Blancan and Irvingtonian faunas, as well as composite faunal lists for the early and late Rancholabrean. We have limited the mammalian faunas listed in Table 2 to those represented by ten or more diagnostic

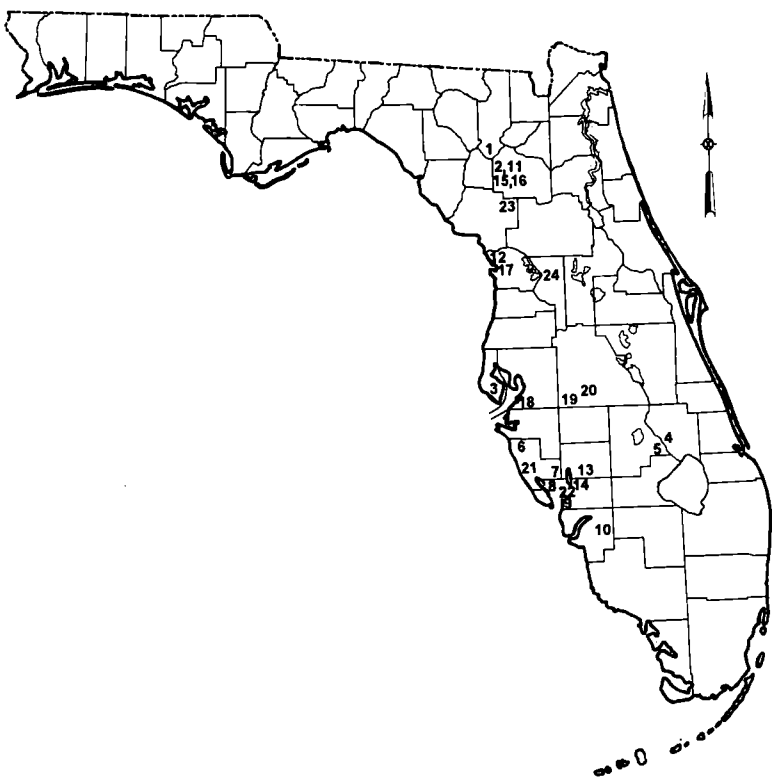

Figure 4. Map of Florida showing location of Blancan and Irvingtonian vertebrate faunas discussed in text. Late Blancan: 1. Santa Fe River 1, 2, 4A, 8A, and 15A, Columbia County; 2. Haile 15A, Alachua County; 3. St. Peterburg Times, Pinellas County; 4. Kissimmee River, Okeechobee County; 5. Brighton Canal, Highlands County; 6. Macasphalt Shell Pit, Sarasota County; 7. Bass Point Waterway, Sarasota County; 8. El Jobean, Charlotte County; 9. Acline Shell Pit, Charlotte County; 10. Lehigh Acres, Lee County; latest Blancan: 11. Haile 7C, Alachua County; earliest Irvingtonian: 12. Inglis 1A, Citrus County; 13. De Soto Shell Pit, De Soto County; 14. Forsberg Shell Pit, Charlotte County; late early Irvingtonian: 15. Haile 16A, Alachua County; 16. Haile 21A, Alachua County; 17. Crystal River Power Plant, Citrus County; 18. Leisey Shell Pit, Hillsborough County; 19. Payne Creek Mine, Polk County; 20. Pool Branch, Polk County; 21. Rigby Shell Pit, Sarasota County; 22. Punta Gorda, Charlotte County; middle Irvingtonian: 23. McLeod Limerock Mine, Levy County; late Irvingtonian: 24. Coleman 2A, Sumter County.

species, which excludes several small, biochronologically significant faunas. These faunas will be briefly discussed after the summaries of the larger sites. Figure 5 is a correlation chart showing the relative stratigraphic position and age of the major Florida Blancan and Irvingtonian faunas discussed in the text.

DuBar (1958) initiated the use of terrestrial vertebrate fossils for the age determination of Plio-Pleistocene shell beds in Florida; however, he was hindered by the limited diversity of the vertebrate samples available to him. Furthermore, 35 years ago paleontologists had only a limited understanding of Late Cenozoic

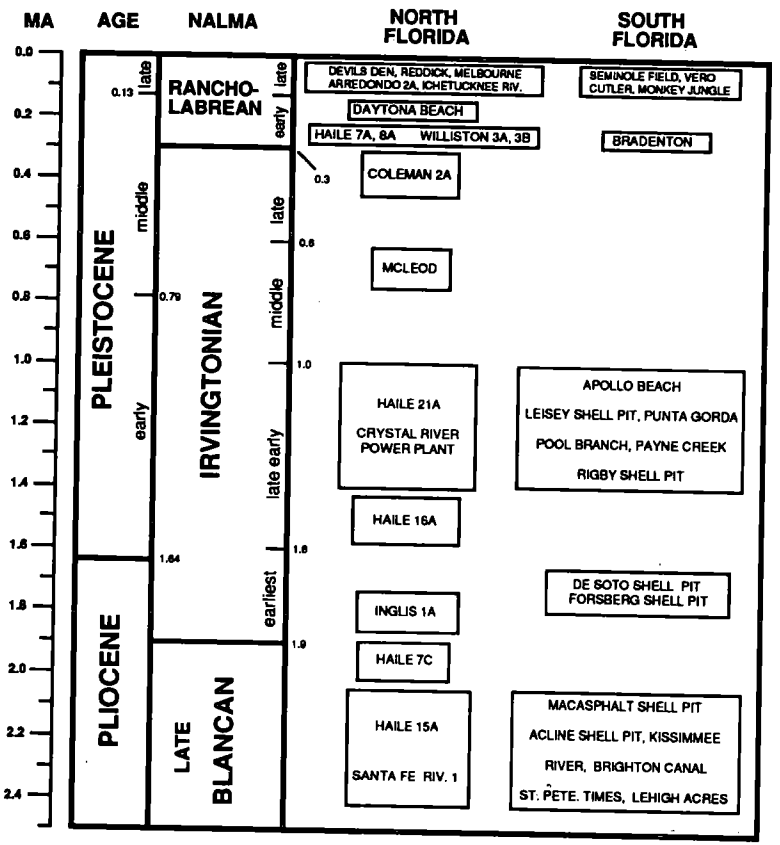

Figure 5. Correlation chart showing relative position and age of the Florida late Pliocene and Pleistocene vertebrate faunas discussed in text. The faunas are divided into those from northern and southern peninsular Florida, with the arbitrary boundary between the two regions placed at 28°N latitude. The faunas listed within a box are approximately equivalent in age, but their order in the box does not represent stratigraphic superposition. Vertical size of boxes expresses the range of possible ages of the sites enclosed in the box.

mammalian chronology in Florida and elsewhere. Webb (1974a) summarized the chronology of Florida late Pliocene and Pleistocene mammals and provided faunal lists for the two Blancan and four Irvingtonian faunas known from the state at that time. In the past decade, large and taxonomically diverse samples of Blancan and Irvingtonian vertebrate fossils have been collected from Florida in direct stratigraphic context with well known marine units (see Table 4) including: Pinecrest Beds (Macasphalt Shell Pit, Morgan and Ridgway 1987; Hulbert 1988a; Emslie 1992a,b; this paper), Caloosahatchee Formation (De Soto Shell Pit, this paper), and Bermont Formation (Leisey and Rigby Shell Pits, Hulbert and Morgan 1989; Webb et al. 1989; papers in this volume). Furthermore, the Late Cenozoic mammalian biochronology of North America has vastly improved over the past 20 years, thanks to the studies of Skinner and Hibbard (1972), Webb (1974a), Lindsay et al. (1975), Kurtén and Anderson (1980), Repenning (1980 1987), Lundelius et al. (1987), and many others.

BLANCAN

There is a 2-million-year gap in the Florida terrestrial vertebrate record between the well known early Pliocene (late Hemphillian) faunas of the Bone Valley Formation (5.2 to 4.5 Ma) and various late Pliocene (late Blancan) faunas (2.5-2.0 Ma).. Although early Blancan terrestrial faunas are unknown from Florida (Morgan and Ridgway 1987), the marine Bee Ridge Fauna from Sarasota County in southwestern Florida (Morgan 1994) appears to be between 3.5 and 3.0 Ma in age (=Blancan III or IV of Repenning 1987). The Bee Ridge Fauna consists exclusively of cetaceans, pinnipeds, and other marine vertebrates that are not comparable with continental faunas of early Blancan age from western North America. The oldest faunas considered in our study are late Blancan in age (Blancan V of Repenning 1987). The two most widely cited reviews of Florida Pliocene and Pleistocene faunas list only two late Blancan vertebrate faunas from the state, Haile 15A and Santa Fe River 1 (Webb 1974a; Kurtén and Anderson 1980). Reasonably complete mammalian faunal lists have been published for both of these sites (Webb 1974a; Robertson 1976). Morgan and Ridgway (1987) described the late Blancan St. Petersburg Times LF from Pinellas County along the central Gulf Coast. They also discussed several other smaller Blancan faunas and presented a brief review of Florida Blancan sites. Numerous recent publications have discussed the late Blancan vertebrate fauna from the Macasphalt Shell Pit in Sarasota County (Morgan and Ridgway 1987; Hulbert 1988a; Jones et al. 1991; Emslie 1992a,b).

Table 4. Florida Blancan and Irvingtonian vertebrate faunas collected in stratigraphic superposition with or in association with marine geologic units.

Formation	Age	Site	Remarks
Pinecrest Beds Tamiami Formation	late Pliocene (2.5-2.0 Ma)	Macasphalt Shell Pit	Collected in place from Unit 4 of Petuch (1982) within Pinecrest Beds
Pinecrest Beds Tamiami Formation	late Pliocene (2.5-2.0 Ma)	Kissimmee River	Not collected in place, associated molluscan fauna typical of Pinecrest Beds
Pinecrest Beds Tamiami Formation	late Pliocene (2.5-2.0 Ma)	St. Petersburg Times	Collected in place immediately above Pinecrest Beds
Pinecrest Beds Tamiami Formation	late Pliocene (2.5-2.0 Ma)	Lehigh Acres	Not collected in place, associated molluscan fauna typical of Pinecrest Beds
Pinecrest Beds Tamiami Formation	late Pliocene (2.5-2.0 Ma)	Brighton Canal	Not collected in place, associated molluscan fauna typical of Pinecrest Beds
Pinecrest Beds Tamiami Formation	late Pliocene (2.5-2.0 Ma)	Acline Shell Pit	Collected in place from Pinecrest Beds
Caloosahatchee Formation	latest Pliocene (2.0-1.6 Ma)	De Soto Shell Pit	Collected in place within Caloosahatchee Fm.
Caloosahatchee Formation	latest Pliocene (2.0-1.6 Ma)	Forsberg Shell Pit[1]	Collected in place within or underlying Caloosahatchee Fm.
Bermont Formation	early Pleistocene (1.6-1.0 Ma)	Leisey Shell Pit	Collected in place within Bermont Fm.
Bermont Formation	early Pleistocene (1.6-1.0 Ma)	Crystal River Power Plant	Collected in place within Bermont Fm.
Bermont Formation	early Pleistocene (1.6-1.0 Ma)	Rigby Shell Pit	Collected in place within Bermont Fm.
Bermont Formation	early Pleistocene (1.6-1.0 Ma)	Punta Gorda LF[2] of Webb (1974a)	Collected in place above Bermont Fm.

[1]The Forsberg Shell Pit and Punta Gorda locality of Waldrop and Wilson (1990) are the same site. However, this is a different locality from the Punta Gorda Local Fauna of Webb (1974a) and Kurtén and Anderson (1980).
[2] = Gomphothere Site of Brooks (1968).

Santa Fe River 1.–The Santa Fe sites are river bottom deposits in northern peninsular Florida collected along an approximately 10 km stretch of the Santa Fe River, which forms the border between Columbia County on the north and Gilchrist County on the south (Fig. 4, site 1). The Santa Fe River 1 LF, including sites 1, 1A, and 1B, was collected from a bend in the river less than 0.5 km in length. The bottom of the Santa Fe River in this region produces a mixture of Blancan and Rancholabrean vertebrates. It is not difficult to separate the faunas of these two ages because there is very little overlap between them with regard to chronologically significant mammals. Although the Santa Fe 1B site was originally thought to be a purely Blancan assemblage (Webb 1974a), a re-examination of the material from this locality reveals the presence of several Rancholabrean taxa, including *Megalonyx jeffersonii*, *Holemsina septentrionalis*, *Castoroides ohioensis*, and *Mammuthus columbi*.

The Santa Fe River 1 site has produced one of the most diverse faunas of large mammals known from the late Blancan of Florida (Table 2), including at least 22 species. Blancan indicators include *Borophagus diversidens*, *Canis lepophagus*, *Nannippus peninsulatus*, *Equus* (*Dolichohippus*), *Platygonus bicalcaratus*, *Hemiauchenia blancoensis*, and *Rhynchotherium praecursor*. The co-occurrence of these taxa with the Neotropical immigrants *Dasypus bellus* (small Blancan form), *Holmesina floridanus* (small Blancan form), *Glyptotherium arizonae*, *"Glossotherium" chapadmalense*, and *Titanis walleri* indicates a post-interchange late Blancan fauna. Five species from the Santa Fe River 1 LF are characteristic of Florida late Blancan and earliest Irvingtonian faunas: *Glyptotherium arizonae*, the dwarf Florida form of *Megalonyx leptostomus*, *Chasmaporthetes ossifragus*, *Capromeryx arizonensis*, and *Titanis walleri*. Santa Fe 1 is one of four Florida late Blancan localities in which *Smilodon* is present (Berta 1987), a genus that does not appear until the early Irvingtonian in the western United States (Lundelius et al. 1987).

General discussions of the Santa Fe River fauna can be found in Webb (1974a), Robertson (1976), Kurtén and Anderson (1980), and Morgan and Ridgway (1987). Taxonomic references to Blancan vertebrate taxa from the Santa Fe River 1 LF include Weaver and Robertson (1967) on the turtle *Trachemys platymarginata*; Brodkorb (1963) on *Titanis walleri* (type locality); Gillette and Ray (1981) on *Glyptotherium arizonae*; Robertson (1976), Edmund (1987), and Hulbert and Morgan (1993) on *Holmesina floridanus*; Kurtén (1965) and Berta (1987) on *Smilodon gracilis*; Berta (1981) on *Chasmaporthetes ossifragus*; and MacFadden and Waldrop (1980) on *Nannippus peninsulatus*.

Blancan mammals also have been reported from three additional Santa Fe River sites. MacFadden and Waldrop (1980) recorded *Nannippus phlegon* (=*N. peninsulatus*) from Santa Fe River 4A, a fauna that also includes *Equus* (*Dolichohippus*), *Capromeryx arizonensis*, and *Platygonus bicalcaratus*. In their review of the Blancan mustelid *Trigonictis*, Ray et al. (1981) described and figured

specimens of *T. macrodon* from Santa Fe River 8A. Berta (1981) reported and figured a maxilla of the hyaenid *Chasmaporthetes ossifragus* from Santa Fe River 15.

Haile 15A.--The Haile 15A LF was deposited in a fissure filling in the late Eocene Crystal River Formation near Newberry, Alachua County (Fig. 4, site 2). This site is located about 30 m above sea level and about 80 km inland from the Gulf of Mexico. Along with abundant freshwater and terrestrial vertebrates, the Haile 15A LF contains a substantial fauna of estuarine and nearshore marine fishes which led Robertson (1976) to propose that it was deposited during a period of high sea level. However, Opdyke et al. (1984) provided data suggesting that the limestone karst region of northern peninsular Florida may have undergone epeirogenic uplift during the Pleistocene. Despite the possibility of some isostatic uplift in response to karstification, it still seems highly probable that the Haile 15A site was deposited during a period when sea level was higher than present. Biochronological data from the vertebrate fauna suggests an age between 2.5 and 2.0 Ma for Haile 15A. Evidence from both eustatic sea level curves (Haq et al. 1987) and the oxygen isotope record (Shackleton and Opdyke 1977) indicates that this 0.5 million year time interval was a period of generally low worldwide sea levels. However, there were several glacial-interglacial cycles during the late Pliocene, with periods of normal or higher than modern sea level at approximately 2.3 and 2.1 Ma (Shackleton and Opdyke 1977). Which of these presumed late Pliocene high sea level stands best approximates the age of Haile 15A, and other Florida late Blancan high sea level faunas discussed below, is problematic at the present time.

The Haile 15A LF has 23 species of mammals, including four taxa characteristic of western Blancan faunas, *Sigmodon medius*, *Nannippus peninsulatus*, *Equus* (*Dolichohippus*), and the otter *Satherium piscinarium*. Haile 15A also records the association of typical Blancan mammals with South American immigrants, thereby indicating a post-interchange late Blancan fauna. Neotropical immigrants present at Haile 15A include *Dasypus bellus* (small Blancan form), *Holmesina floridanus* (type locality), "*Glossotherium*" *chapadmalense*, and *Hydrochaeris holmesi*. Haile 15A also records late occurrences of two species known from the late Hemphillian (earliest Pliocene) Palmetto Fauna in central Florida, the flying squirrel *Cryptopterus webbi* (type locality; Pratt pers. comm.) and the hipparionine horse *Cormohipparion emsliei* (Hulbert 1988a). Haile 15A is one of the earliest occurrences of *Smilodon gracilis* (see Berta 1987).

Robertson (1976) monographed the Haile 15A mammalian fauna and Campbell (1976) reviewed the avifauna. Additional taxonomic references on this fauna include Weaver and Robertson (1967) on *Trachemys platymarginata* (type locality), Edmund (1987) and Hulbert and Morgan (1993) on *Holmesina*

floridanus, Berta (1987) on *Smilodon gracilis*, Martin (1979) on *Sigmodon medius*, Kinsey (1974) on *Mylohyus floridanus* (type locality), and Webb (1974b) on *Hemiauchenia macrocephala*.

Macasphalt Shell Pit.--The Macasphalt Shell Pit LF was collected from a commercial shell mine operated by the APAC (formerly Macasphalt) Corporation, located 8 km east of Sarasota, Sarasota County (Fig. 4, site 6). The fossil vertebrates from the Macasphalt Shell Pit are derived from a dark brown to blackish sandy organic layer up to 1 m in thickness (unit 4 or "black layer" of Petuch 1982). The vertebrate-bearing unit and the marine shell beds that occur both below and above it are referred to the Pinecrest Beds (Petuch 1982; Stanley 1986), or the Pinecrest Sand Member of the Tamiami Formation of some authors (Hunter 1968; DuBar 1974). Waldrop and Wilson (1990) recently renamed this unit the Fruitville Formation. Measured stratigraphic sections at the Macasphalt Shell Pit place the vertebrate-bearing unit from 5-8 m below the present ground surface. This is near or slightly above present sea level based on the current surface elevation of 7-8 m. Unit 4 contains a rich nearshore marine and estuarine vertebrate and invertebrate fauna providing strong evidence that, like Haile 15A, the Macasphalt Shell Pit LF was deposited during a period of relatively high sea level.

The extraordinarily rich marine molluscan fauna from the Pinecrest Beds exposed in the Macasphalt (=APAC) Shell Pit has prompted numerous studies by invertebrate paleontologists (e.g. Petuch 1982; Stanley 1986; Lyons 1991; Scott and Allmon [eds.] 1992). However, there is by no means complete agreement on the age of the richly fossiliferous marine shell beds directly underlying and overlying the primary bone-bearing horizon. Stanley (1986) regarded these beds to be early Pliocene in age, Lyons (1991) considered them to be middle Pliocene (3.5-3.0 Ma), while others have suggested a late Pliocene age (Ward 1992; Zullo 1992). A recent paper on the integrated geochronology of the Macasphalt Shell Pit (Jones et al. 1991), including analyses of mammalian biochronology, ostracode biostratigraphy, paleomagentic polarity, and strontium isotope stratigraphy, placed the age of the vertebrate-bearing unit 4 at Macasphalt between 2.5 and 2.0 Ma.

The Macasphalt vertebrate fauna, composed of well over 100 species, contains a mixture of marine, estuarine, freshwater, and terrestrial taxa, with the brackish and freshwater component predominating. The mammalian fauna consists of 25 species, including many characteristic Blancan forms: dwarf *Megalonyx leptostomus*, *Trigonictis macrodon*, *Sigmodon medius*, *Nannippus peninsulatus*, *Equus* (*Dolichohippus*), *Platygonus bicalcaratus*, *Hemiauchenia blancoensis*, and *Rhynchotherium* cf. *R. praecursor*. The association of these species, in particular *N. peninsulatus*, in the Macasphalt Shell Pit LF with a diverse suite of Neotropical immigrants, including *Dasypus bellus* (small Blancan form), *Holmesina floridanus* (small Blancan form), "*Glossotherium*"

chadpadmalense, and *Neochoerus dichroplax*, is typical of all well-sampled Florida late Blancan faunas (Morgan and Ridgway 1987).

Morgan and Ridgway (1987) summarized the Macasphalt Shell Pit LF and provided a list of the diagnostic mammals. Macasphalt is the type locality of the hipparionine horse *Cormohipparion emsliei* described by Hulbert (1988a). Prior to its discovery at Macasphalt, the youngest record of *Cormohipparion* was from the late Hemphillian Bone Valley Formation of central Florida. Morgan (1991) reported the molossid bat *Tadarida* cf. *T. brasiliensis* from this site. Jones et al. (1991) briefly mentioned the Macasphalt mammalian fauna in their geochronological discussion of the APAC Shell Pit. Emslie (1992a,b) described the rich avifauna of over 40 taxa from the Macasphalt Shell Pit.

Kissimmee River.--The Kissimmee River LF is derived primarily from UF sites Kissimmee River 5 and 6 located south of Ft. Basinger in Okeechobee County (Fig. 4, site 4). Vertebrate fossils were collected from the Kissimmee River basin in the 1960s and 1970s during and after a project conducted by the U. S. Army Corps of Engineers to channelize the Kissimmee River. The extensive spoil piles produced by the dredging of the river channel have long been known to produce a rich Pliocene molluscan fauna representative of the Pinecrest Beds. Certain Pinecrest localities along the Kissimmee River have produced a fairly diverse Blancan vertebrate fauna as well. Although most of the Kissimmee River LF was collected from spoil piles, primarily by the late Howard Converse, the fossils seem to constitute a uniform late Blancan fauna that compares closely to other Florida samples of this age. The close association of this vertebrate fauna with marine molluscs of the Pinecrest Beds is similar to the situation encountered in the Macasphalt Shell Pit, St. Petersburg Times, Brighton Canal, Lehigh Acres, and Acline Shell Pit sites. The Kissimmee River LF consists of a mixture of terrestrial, freshwater, and marine taxa, suggesting that the site formed in a shallow marine depositional environment. The exact elevation of the vertebrate-bearing unit is unknown; however, the current surface elevation of about 10 m in this region strongly suggests that the fauna was deposited during a period of high sea level.

There are no published references to the Kissimmee River LF, which consists of at least 24 species of mammals. Characteristic Blancan mammals from the Kissimmee River LF include the dwarf *Megalonyx leptostomus*, *Nannippus peninsulatus*, *Equus* (*Dolichohippus*), and *Platygonus bicalcaratus*. Seven species of Neotropical immigrants are present in this fauna, the capybara *Neochoerus dichroplax* and six xenarthrans, *Dasypus bellus* (small Blancan form), *Holmesina floridanus* (small Blancan form), *Glyptotherium arizonae*, *Pachyarmatherium leiseyi*, *"Glossotherium" chapadmalense*, and *Eremotherium* sp. The oldest previous record of *Eremotherium* was from the earliest Irvingtonian Inglis 1A LF (Webb 1974a; Webb and Wilkins 1984). There are now four late Blancan records of *Eremotherium*, including the Kissimmee River, Brighton Canal, and Lehigh

Acres faunas in southern Florida, and the extensive sample from the latest Blancan Haile 7C LF in northern peninsular Florida. The Kissimmee fossils of *Pachyarmatherium leiseyi* constitute the oldest record of this species in Florida. All other Florida occurrences of *P. leiseyi* are from early Irvingtonian faunas. The two osteoderms of this species from the Kissimmee River 6 site were collected from spoil piles, as was the remainder of the fauna, and thus there is a possibility of faunal mixing. However, scutes of *P. leiseyi* are also known from a Blancan fauna in South Carolina in association with *Nannippus* (J. Knight, pers. comm.). The association of typical Blancan mammals with a large suite of Neotropical immigrants in the Kissimmee River fauna places the age of this site as post-Interchange between 2.5 and 2.0 Ma.

Haile 7C.--Vertebrate fossils from the recently discovered Haile 7C LF are preserved in clays and fine-grained sands deposited in a solution feature in the marine Eocene Crystal River Formation in a commercial limestone mine near Newberry, Alachua County (Fig. 4, site 11). The site probably represents either a sinkhole pond or spring and is numerically dominated by freshwater taxa, including anurans, salamanders, the turtles *Trachemys platymarginata* (=*T. idahoensis* of Jackson 1988) and *Chelydra* n. sp., and the alligator *Alligator mississippiensis*. Many of the turtles are represented by complete shells, often including the articulated skulls and limbs. Likewise, several of the mammals from Haile 7C are known from associated or articulated skeletons. The Haile 7C LF includes 16 taxa of mammals. The large mammal fauna is dominated by *Eremotherium*, *Holmesina*, and a new species of *Tapirus* (Hulbert in prep.). Small rodents, carnivores, and most ungulates are very rare in the site. Only two papers have discussed the Haile 7C LF (Hulbert et al. 1989; Hulbert and Morgan 1993).

The age of Haile 7C is still somewhat uncertain because of the limited diversity of the mammalian fauna. The mammals present are indicative of either a latest Blancan or earliest Irvingtonian age, probably dating between 2.2 and 1.7 Ma. A late Blancan age assignment is difficult to substantiate because there are no strictly Blancan mammals present in the fauna. Although the Haile 15A LF is located within 1 km of Haile 7C, the vertebrate faunas from these two sites differ considerably. Haile 7C not only lacks the diagnostic Blancan genera found at Haile 15A, but it also contains no evidence of the marine taxa present in the latter fauna, indicating that Haile 7C was not deposited during the same high sea level stand.

Haile 7C is clearly younger than 2.5 Ma, as it has six genera of Neotropical immigrants, *Dasypus*, *Holmesina*, *Glyptotherium*, *Eremotherium*, *Neochoerus*, and *Erethizon*. *Eremotherium* and *Erethizon* were previously unknown from the Blancan of Florida, although we also report *Eremotherium* from three additional late Blancan faunas in the southern half of the state. *Erethizon* occurs in several late Blancan faunas in the western United States (Harrison 1976; Frazier 1981).

Although turtles are not often regarded as particularly useful index fossils, the large emydid *Trachemys platymarginata* is common in most Florida late Blancan faunas. It is replaced by the smaller *T. scripta* in the early Irvingtonian. The Haile 7C *Trachemys* is essentially identical to the type series of *T. platymarginata* from Haile 15A. Furthermore, Haile 7C and Haile 15A are the only two known localities for a large undescribed species of *Chelydra*.

Lundelius et al. (1987) noted that there is not a sharp faunal break between the Blancan and Irvingtonian, but rather they documented a gradual transition between these two NALMA that occurred between about 2.0 and 1.7 Ma. Thus, it is not surprising that some faunas from this time period are difficult to place in one or the other of these two ages. The absence of typical Blancan genera, such as *Borophagus*, *Nannippus*, and *Equus* (*Dolichohippus*) from Haile 7C argues for an early Irvingtonian age; however, carnivores and horses are virtually absent in this fauna. Perhaps the majority of Florida late Blancan faunas occur in the time period immediately following the onset of the Great American Interchange between 2.5 and 2.2 Ma. If so, there might be a significant period of time, perhaps as long as half a million years between about 2.2 and 1.7 Ma, after the extinction of *Nannippus* and most other typical Blancan taxa, but before the appearance of most diagnostic Irvingtonian taxa. We suggest that the Haile 7C LF dates to the very end of the Blancan during the early portion of the transitional period between the Blancan and Irvingtonian NALMA. Regardless of its placement in the land mammal biochronology, Haile 7C is clearly latest Pliocene in age (younger than 2.5 Ma and older than 1.6 Ma). The Borchers LF in Kansas is a well known fauna that also appears to fall in this transitional time period, and has likewise been regarded as either late Blancan or early Irvingtonian (Lundelius et al. 1987).

Other Florida late Blancan faunas.--Among the Florida Blancan localities reviewed by Morgan and Ridgway (1987) are several important sites, including St. Petersburg Times, Bass Point Waterway, El Jobean, and Acline Shell Pit, not listed in Table 2 because they have fewer than ten diagnostic species of mammals. We briefly discuss several of these smaller sites, as well as the previously unpublished Brighton Canal and Lehigh Acres local faunas. Most of these sites possess critical Blancan taxa or occur in stratigraphic superposition with well known marine units.

The St. Petersburg Times Site is located about 10 km inland from the Gulf of Mexico in downtown St. Petersburg, Pinellas County (Fig. 4, site 3). The vertebrate fossils constituting the St. Petersburg Times LF were recovered from a black sandy organic layer near the bottom of a borrow pit. Underlying the bone-bearing layer was a semi-indurated marine shell bed tentatively referred to the Pinecrest Beds based on its molluscan fauna. The vertebrate unit was about 12-15 m below the surface, and thus was near present sea level based on current surface elevations. The stratigraphic sequence and the absence of marine taxa in the St. Petersburg Times Site both suggest deposition during a period of low sea level.

The vertebrate fauna from the St. Petersburg Times Site consists of 30 species and is dominated by freshwater forms, especially sirens, water snakes, turtles, and aquatic birds. Nine species of terrestrial mammals occur in the St. Petersburg Times LF (Morgan and Ridgway 1987), four of which are characteristic of Florida late Blancan faunas, *Holmesina floridanus*, *Glyptotherium arizonae*, small *Megalonyx leptostomus*, and *Nannippus peninsulatus*. Morgan and Ridgway (1987) also reviewed the lower vertebrates in the St. Petersburg Times LF. Becker (1987) and Emslie (1992a) discussed the avifauna.

The Lehigh Acres LF is here designated for a vertebrate fauna collected by Thomas Missimer from the Lehigh Corporation Pits south of Alva, Lee County (Fig. 4, site 10). The fossils were derived from a semi-indurated calcareous marl containing a mixture of marine and freshwater molluscs characteristic of the Pinecrest Beds. Although collected primarily from spoil piles, there is no indication that the fauna is mixed. The Lehigh Acres LF is composed of 22 species of vertebrates, including nearshore marine, freshwater, and terrestrial species. There are nine species of terrestrial mammals in the fauna, including four typical Blancan taxa, "*Glossotherium*" *chapadmalense*, *Nannippus peninsulatus*, *Equus* (*Dolichohippus*), and *Platygonus bicalcaratus*. The association of *Nannippus* with "*Glossotherium*" and *Eremotherium* characterizes a post-Interchange late Blancan fauna. The *Eremotherium* from Lehigh Acres represents one of the few Blancan records for this genus.

The Brighton Canal LF is a small, previously undescribed late Blancan vertebrate fauna collected by Muriel Hunter from spoil piles along the Brighton Canal near Brighton, Highlands County (Fig. 4, site 5). The predominant stratigraphic unit in this region of the canal is the Pinecrest Beds, based on the molluscan fauna collected from the same spoil piles that produced the vertebrates. The Brighton Canal LF includes nine species of terrestrial mammals, four of which are characteristic of Florida late Blancan faunas, *Glyptotherium arizonae*, *Nannippus peninsulatus*, *Equus* (*Dolichohippus*), and *Mylohyus floridanus*. The South American immigrant *Eremotherium* is also present.

The Bass Point Waterway 1 LF, Sarasota County (Fig. 4, site 7), includes *Holmesina floridanus*, *Smilodon gracilis*, *Nannippus peninsulatus*, and *Equus* (*Dolichohippus*). The nearby El Jobean LF in Charlotte County (Fig. 4, site 8) also contains *Holmesina floridanus*, *Smilodon gracilis*, and *Nannippus peninsulatus*. These two sites were first mentioned by Churcher (1984) is his review of *Ischyrosmilus gracilis* (=*Smilodon gracilis* following Berta 1987) from Florida. The association of *Nannippus* and *Holmesina* is diagnostic of most Florida post-Interchange late Blancan faunas. The Bass Point Waterway and El Jobean sites are among the earliest records for *Smilodon gracilis*.

The Acline Shell Pit, located near Acline in Charlotte County (Fig. 4, site 9), has produced a small Blancan fauna from marine shell beds referred to the Pinecrest Beds (Olsson and Petit 1964). The most diagnostic mammals in the

Acline fauna are "*Glossotherium*" *chapadmalense* and *Cuvieronius tropicus*. Morgan and Ridgway (1987) mentioned four additional late Blancan vertebrate faunas from southwestern Florida not discussed here, including Sommers Pit and Northport in Sarasota County, Port Charlotte in Charlotte County, and Mule Pen Quarry in Collier County.

IRVINGTONIAN

Webb (1974a) and Kurtén and Anderson (1980) listed only four Irvingtonian faunas from Florida: Inglis 1A, Punta Gorda, Pool Branch, and Coleman 2A. Inglis 1A (Klein 1971; Webb 1974a; Webb and Wilkins 1984) and Coleman 2A (Martin 1974) both have diverse mammalian faunas composed of more than 40 species, whereas Punta Gorda and Pool Branch have much smaller faunas consisting primarily of large mammals. A fifth Florida Irvingtonian site, Haile 16A, has been mentioned numerous times in taxonomic papers, but no published mammalian faunal list is available.

Earliest Irvingtonian faunas (2.0-1.6 Ma), including Inglis 1A and De Soto Shell Pit, contain many taxa typical of late Blancan faunas and lack *Mammuthus* which does not arrive in North America until after 1.6 Ma. Late early Irvingtonian faunas (1.6-1.0), such as Leisey, usually have *Mammuthus hayi*, lack most Blancan holdovers, and possess a number of taxa also typical of middle Irvingtonian faunas. We use the term early Irvingtonian in the context of Lundelius et al. (1987) only when discussing faunas of both the earliest and late early Irvingtonian (i.e., 2.0 to 1.0 Ma). The middle Irvingtonian encompasses the interval from 1.0 to 0.6 Ma, and the late Irvingtonian is from 0.6 to 0.3 Ma. The reasons for locating the boundaries at these dates are presented above.

Inglis 1A.--The Inglis 1A LF was collected from a solution cavity in the Eocene Inglis Formation along the now-defunct Cross Florida Barge Canal in Citrus County (Fig. 4, site 12). The Inglis 1A site occurs in a karst solution feature that is as much as 5 m below present mean sea level. However, the fauna totally lacks marine forms, suggesting that it was deposited during a period of low sea level. Richmond and Fullerton (1986) recorded a glacial interval from 2.01 to 1.87 Ma (corresponding to marine oxygen isotope stage 40); this age is in agreement with that provided by vertebrate biochronology (see below). Correlation of Inglis 1A with a glacial period is supported by certain taxa in the vertebrate fauna that suggest cooler and/or more arid conditions (Carr 1980; Meylan 1982; Webb and Wilkins 1984; Morgan 1991).

Our list of mammals from Inglis 1A (Table 2) includes several additions and corrections to the published mammalian fauna for this site (Webb 1974a; Webb

and Wilkins 1984). The Inglis mammal fauna consists of 53 species, with the best represented forms being xenarthrans, carnivores, ungulates, and small mammals. Inglis 1A possesses several genera listed by Lundelius et al. (1987) as characteristic of the Irvingtonian, including *Smilodon*, *Lepus*, and *Equus* (s.s.), and lacks *Borophagus*, *Nannippus*, *Equus* (*Dolichohippus*), *Rhynchotherium*, and other genera restricted to the Blancan. However, Inglis 1A does share a number of taxa with Florida late Blancan faunas, including *Glyptotherium arizonae*, the dwarf Florida form of *Megalonyx leptostomus*, *Trigonictis macrodon*, *Chasmaporthetes ossifragus*, *Geomys propinetis*, *Sylvilagus webbi*, *Capromeryx arizonensis*, and the phororhacid bird *Titanis walleri*. The presence of both Blancan holdovers and characteristic Irvingtonian taxa, as well as the absence of *Mammuthus*, indicates an earliest Irvingtonian age (2.0-1.6 Ma) for Inglis 1A. The mammals from Inglis 1A compare closely to the fauna from Curtis Ranch in Arizona (Lindsay and Tessman 1974). Diagnostic mammals shared by these two faunas include *Glyptotherium arizonae*, *Canis edwardii*, *Sigmodon curtisi*, *Ondatra idahoensis*, and *Capromeryx arizonensis*.

The geology and stratigraphy of the Inglis deposit were discussed by Klein (1971), who also reviewed the carnivores and ungulates. The birds (Carr 1980) and squamate reptiles (Meylan 1982) of Inglis 1A have been studied in detail. There are numerous taxonomic references on mammals from the Inglis 1A LF, including Gillette and Ray (1981) on *Glyptotherium arizonae*, McDonald (1977) on *Megalonyx leptostomus*, Morgan et al. (1988) on *Desmodus archaeodaptes*, Morgan (1991) on the chiropteran fauna, Ray et al. (1981) on *Trigonictis macrodon*, Berta (1981) on *Chasmaporthetes ossifragus*, Berta (1987) on *Smilodon gracilis*, Van Valkenburgh et al. (1990) on *Miracinonyx inexpectatus*, Frazier (1981) on *Erethizon kleini* (type locality), Ahearn (1981) on *Hydrochaeris holmesi*, Wilkins (1984) on *Geomys propinetis* (type locality), Martin (1979) on *Sigmodon curtisi*, and White (1991) on *Sylvilagus webbi* (type locality).

De Soto Shell Pit.--The De Soto Shell Pit LF is here designated for the vertebrate fauna collected from organic layers in the Caloosahatchee Formation exposed in three commercial shell mines south of Arcadia in De Soto County (Fig. 4, site 13). This is the first published reference to the De Soto Shell Pit LF. The mammalian fauna from the De Soto Shell Pit is composed of 32 species (see Table 2), 25 of which are in common with Inglis 1A. The biochronologically significant species of mammals shared by the De Soto and Inglis faunas are: *Glyptotherium arizonae*, small *Megalonyx leptostomus*, *Canis edwardii*, *Trigonictis macrodon*, *Chasmaporthetes ossifragus*, *Geomys propinetis*, *Ondatra idahoensis*, *Sigmodon curtisi*, *Capromeryx arizonensis*, an undescribed dwarf species of *Hemiauchenia*, and an undescribed species of *Tapirus*. Like Inglis, the De Soto fauna lacks genera restricted to the Blancan, but has a number of taxa common to both Florida late Blancan and earliest Irvingtonian faunas, has *Equus* (s.s.) rather than *Equus*

(*Dolichohippus*), and lacks *Mammuthus*. The common De Soto emydid turtle is *Trachemys platymarginata*, a species limited to the late Blancan and earliest Irvingtonian in Florida. All of these factors taken together strongly indicate an earliest Irvingtonian age. The earliest occurrence of the arvicoline rodent *Atopomys* appears to be in the De Soto Shell Pit LF. This genus is also known from the late early Irvingtonian Haile 16A LF. Elsewhere in North America *Atopomys* is not known prior to the middle Irvingtonian (Winkler and Grady 1990).

The De Soto Shell Pit LF contains a number of nearshore marine taxa, including sharks, bony fishes, and the monk seal *Monachus*, indicating that the site probably formed near sea level. Therefore, the Inglis 1A and De Soto Shell Pit local faunas are not quite the same age. Inglis was deposited below present sea level during a glacial interval, while De Soto was deposited about 5-10 m above modern sea level during an interglacial. Based on the oxygen isotope record (Shackleton and Opdyke 1977), the only high sea level stand during the latest Pliocene occurred about 1.8 Ma. Independent evidence for the age of the De Soto Shell Pit LF comes from the rich marine molluscan fauna of the Caloosahatchee Formation that occurs in direct stratigraphic superposition both below and above the units containing the vertebrate fauna. Lyons (1991) considered the entire molluscan fauna of the Caloosahatchee Formation to be late Pliocene in age (older than 1.8 Ma). Corals collected near "the top of the Caloosahatchee" Formation along the Caloosahatchee River have yielded Helium/Uranium dates of 1.89 to 1.78 Ma (Bender 1973). These dates are consistent with the earliest Irvingtonian (2.0-1.6 Ma) age suggested by the De Soto Shell Pit vertebrate fauna.

Haile 16A.--The Haile 16A LF is located in the Haile Quarry complex northeast of Newberry, Alachua County (Fig. 4, site 15). The fossils were derived from massive dark, silty clays filling a large fissure formed in marine limestones referred to the Eocene Crystal River Formation. The depth, areal extent, and stratigraphy of the Haile 16A locality could not be determined since the site was destroyed by mining operations before it could be properly excavated. Although all fossils from this site were obtained by collecting and screenwashing spoil piles, there is no indication that the fauna is mixed. Like many other northern Florida karst deposits, Haile 16A has an unbalanced mammal fauna. The most abundant large mammals are the ground sloths *Eremotherium*, *Megalonyx*, and *Paramylodon*, and the tremarctine bear *Arctodus pristinus*. Ungulates are uncommon in this fauna and proboscideans are absent. The microvertebrate fauna from Haile 16A is extremely abundant and taxonomically diverse, including large samples of insectivores, bats, and rodents, as well as birds, snakes, lizards, and frogs.

No faunal list from Haile 16A has been published, but at least 33 species of mammals are known to be present (Table 2). Because the small mammals from

this site have not been completely studied, the actual number of species present is probably somewhat higher. Haile 16A has been regarded as middle Irvingtonian by most previous authors (Frazier 1981; Morgan et al. 1988; Winkler and Grady 1990; Morgan 1991), although Lundelius et al. (1987) questionably placed this fauna in the late Irvingtonian. A detailed analysis of the mammalian fauna from Haile 16A suggests that a late early Irvingtonian age is more likely. The *Holmesina* from Haile 16A is similar in size to individuals of *H. floridanus* from Inglis 1A and Leisey, and is distinctly smaller than specimens referred to *H. septentrionalis* from the middle Irvingtonian McLeod Limerock Mine (Hulbert and Morgan 1993). The largest available sample of the newly described armadillo *Pachyarmatherium* (Downing and White this volume) is actually from Haile 16A not Leisey. It appears to be restricted to late Blancan and early Irvingtonian faunas in Florida. The cotton rat *Sigmodon libitinus* is known from Haile 16A (type locality), as well as the early Irvingtonian Leisey Shell Pit and Payne Creek Mine local faunas. Other biochronologically diagnostic species shared by Haile 16A and Leisey Shell Pit include: *Megalonyx wheatleyi; Erethizon dorsatum*; undescribed species of *Podomys*, *Pedomys*, and *Synaptomys*; *Tapirus haysii*; *Equus "fraternus*;" and *Palaeolama mirifica*. All of these species are absent from Florida earliest Irvingtonian faunas, although several do occur in middle Irvingtonian and younger sites. Although its biochronological significance is unknown, the only known Florida occurrence of the zapodid rodent *Zapus* is from Haile 16A.

Three species of mammals from Haile 16A indicate that this site is slightly older than Leisey: *Trigonictis* cf. *T. cookii*, *Geomys propinetis*, and *Sylvilagus webbi*. The mustelid *Trigonictis* has been considered a Blancan indicator in western faunas (e.g. Kurtén and Anderson 1980). However, the presence of *T. cookii* at Haile 16A and *T. macrodon* in the Inglis 1A and De Soto Shell Pit local faunas (Ray et al. 1981) confirms that this genus survived into the early Irvingtonian in eastern North America. With the exception of Haile 16A, *Sylvilagus webbi* and *Geomys propinetis* are both restricted to Florida late Blancan and earliest Irvingtonian faunas. Winkler and Grady (1990) regarded the arvicoline rodent *Atopomys* as characteristic of middle Irvingtonian faunas. The presence of *Atopomys* in the early Irvingtonian Haile 16A and De Soto Shell Pit local faunas strongly indicates that this rare genus evolved considerably earlier than previously thought. Although Haile 16A shares several taxa with Florida late Blancan and earliest Irvingtonian faunas, on the whole this fauna has more species in common with Leisey and other late early Irvingtonian sites. The Haile 16A LF probably derives from the early half of the late early Irvingtonian (1.6 to 1.3 Ma), and is intermediate in age between earliest Irvingtonian faunas such as Inglis 1A and late early Irvingtonian faunas like Leisey.

Many taxonomic publications have mentioned mammals from Haile 16A including Edmund (1987) and Hulbert and Morgan (1993) on *Holmesina*, Downing and White (this volume) on *Pachyarmatherium*, McDonald (1977) on

Megalonyx wheatleyi, Morgan et al. (1988) and Morgan (1991) on *Desmodus archaeodaptes*, Emslie (this volume) on *Arctodus pristinus*, Ray et al. (1981) on *Trigonictis* cf. *T. cookii*, Wilkins (1984) on *Geomys propinetis*, Frazier (1981) on *Erethizon dorsatum*, Martin (1979) on *Sigmodon libitinus*, Winkler and Grady (1990) on *Atopomys salvelinus*, and Hulbert (this volume) on *Tapirus haysii* and *Equus "fraternus."*

Pool Branch.--The Pool Branch LF was collected from the banks of Pool Branch, a tributary of the Peace River in Polk County (Fig. 4, site 21). The Pool Branch mammalian fauna was first listed by Webb (1974a) and later updated by McDonald (1985). Pool Branch was one of only four Irvingtonian faunas discussed by Webb (1974a) and Kurtén and Anderson (1980). Papers mentioning taxa from this fauna include Webb (1974b) on *Hemiauchenia macrocephala*, McDonald (1985) on *Nothrotheriops*, and Hulbert (this volume) on *Equus* and *Tapirus*.

Twelve species of mammals from Pool Branch are listed in Table 2. Carnivores are absent and small mammals are represented only by two partial rodent teeth, both referable to the arvicoline *Ondatra annectens*. This species of muskrat also occurs at Leisey and is characteristic of early and middle Irvingtonian faunas. The giant tapir, *Tapirus haysii*, is restricted to late early and middle Irvingtonian faunas in Florida (Hulbert this volume). McDonald (1985) reported and figured a number of postcranial elements of the ground sloth *Nothrotheriops* from Pool Branch, the first record of this genus from eastern North America. A much larger sample of this sloth, now referred to *N. texanus*, has been recovered from the Leisey Shell Pit LF (McDonald this volume). Another similarity between Leisey and Pool Branch is the presence of an undescribed species of hemionine horse, *Equus* (*Hemionus*) sp. (Hulbert this volume). All 12 species of mammals listed from Pool Branch in Table 2 also occur at Leisey strongly indicating a late early Irvingtonian age.

Payne Creek Mine.--An interesting and mostly unstudied vertebrate fauna has been collected from the Payne Creek Mine, located in Polk County about 10 km southwest of Pool Branch (Fig. 4, site 20). Steadman (1984) reported 10 avian taxa from the Payne Creek Mine LF, including an extralimital record of the least grebe, *Podiceps dominicus*. The mammalian fauna from the Payne Creek Mine consists of at least 22 species, including several typical early Irvingtonian xenarthrans and rodents (Table 2). There are four diagnostic species of xenarthrans from the Payne Creek Mine, *Holmesina floridanus*, *Pachyarmatherium leiseyi*, *Megalonyx wheatleyi*, and *Eremotherium* n. sp. The stage of evolution of the *H. floridanus* osteoderms from Payne Creek is suggestive of an early Irvingtonian age. The new species of *Eremotherium* is characteristic of Florida late Blancan and early Irvingtonian faunas (De Iuliis and Cartelle in prep). *Megalonyx wheatleyi* appears to be restricted to late early and middle Irvingtonian

faunas. This fauna also contains the typical Florida Irvingtonian tremarctine bear, *Arctodus pristinus*. The Payne Creek Mine LF has a diverse assemblage of small mammals, including the cotton rat *Sigmodon libitinus* and two species of arvicolines, the muskrat *Ondatra annectens* and an undescribed species of the vole *Pedomys* (see Morgan and White this volume). All three of these species also are present in the Leisey Shell Pit and Haile 16A local faunas. The similarity of the Payne Creek Mine fauna to that of Leisey strongly indicates a late early Irvingtonian age (probably between 1.3 and 1.0 Ma).

Crystal River Power Plant.--The Crystal River Power Plant LF was discovered during the construction of the Crystal River Nuclear Power Plant, located just inland from the Gulf of Mexico about 6 km west of Red Level in Citrus County (Fig. 4, site 17). Vertebrate fossils were encountered about 10 m below present sea level beneath an extensive marine shell bed. The marine molluscan fauna from this shell bed is very similar to that from Leisey, and is probably equivalent to the Bermont Formation. The vertebrate fauna contains a large sample of freshwater fish, but no marine forms are present. The absence of marine vertebrates, coupled with the fact that the site was discovered well below present sea level, provides strong evidence that the Crystal River Power Plant LF was deposited during a glacial interval.

The mammalian fauna from the Crystal River Power Plant LF is composed of 16 species (Table 2). The presence of *Lutra* and *Castoroides* confirms a post-Blancan age for this site as both genera first appear in the Irvingtonian. Species characteristic of Florida Irvingtonian faunas include *Arctodus pristinus*, a large species of *Procyon*, *Tapirus haysii*, and *Equus "leidyi."* Several taxa from Crystal River further restrict the age of this fauna within the Irvingtonian. The presence of *Smilodon gracilis* and *Tapirus haysii* rules out a late Irvingtonian age. One of the most diagnostic mammals in the Crystal River Power Plant LF is the canid *Canis edwardii*, a species restricted to the early Irvingtonian. The stage of evolution represented by the small sample of *Holmesina* osteoderms from Crystal River is also consistent with an early Irvingtonian age (Hulbert and Morgan 1993). *Megalonyx wheatleyi* is now known from four Florida late early Irvingtonian faunas, including Crystal River. Every species of mammal listed in Table 2 from from Crystal River occurs at Leisey as well, suggesting that these two faunas are very similar in age.

Rigby Shell Pit.--The Rigby Shell Pit LF was collected from a commercial shell mine near Nokomis, Sarasota County (Fig. 4, site 22). The vertebrate fossils were derived from a unit within marine shell beds of the Bermont Formation and consist of a mixture of marine, freshwater, and terrestrial species. The most abundant large vertebrates in the fauna are *Hemiauchenia macrocephala* and

Equus "leidyi." The Rigby Shell Pit fauna was briefly mentioned by Hulbert and Morgan (1989), but no published faunal list is available.

All 12 species of mammals identified from Rigby are also known from Leisey, five of which are indicative of an Irvingtonian age. *Arctodus pristinus* and *Equus "leidyi"* are typical of many Florida Irvingtonian faunas, but do not provide a more precise age refinement. The most age diagnostic mammal from Rigby is *Canis edwardii*, which is restricted to early Irvingtonian sites in Florida. A distal humerus of *Holmesina floridanus* from Rigby is distinctly larger than comparable specimens from Leisey, suggesting that the Rigby Shell Pit may be slightly younger (Hulbert and Morgan 1993). Except for the larger size of *Holmesina*, the mammalian fauna from Rigby is indistinguishable from that of the Leisey Shell Pit and is probably late early Irvingtonian in age as well.

Haile 21A.--The Haile 21A LF is located in the Haile Quarry complex northeast of Newberry in Alachua County (Fig. 4, site 16). The site consisted of clays, sands, and limestone breccias filling a karst solution cavity in the marine late Eocene Crystal River Formation. This locality has been completely destroyed by mining operations. Morgan et al. (1988) and Morgan (1991) briefly discussed the Haile 21A site and its vertebrate fauna. The mammalian fauna from Haile 21A consists of 20 species, but is overwhelmingly dominated by the large peccary, *Platygonus vetus* (Wright this volume). Haile 21A is the type locality of the primitive vampire bat, *Desmodus archaeodaptes* (Morgan et al. 1988), and also has a large sample of the vespertilionid bat *Myotis austroriparius*. In contrast to most other north Florida Irvingtonian karst deposits, small mammals are scarce in the Haile 21A LF, with the exception of bats.

Tapirus haysii, *Equus "leidyi,"* *Platygonus vetus*, and a large species of *Procyon* occur in the Haile 21A LF, all of which are limited to the Irvingtonian in Florida. Furthermore, *Tapirus haysii*, has not yet been recorded from either earliest Irvingtonian or late Irvingtonian faunas (Hulbert this volume), thereby limiting the age of Haile 21A to late early or middle Irvingtonian. The presence of *Canis edwardii* in the Haile 21A LF (Berta this volume) strongly suggests an early Irvingtonian age. Haile 21A is the only other Florida fauna besides Leisey in which both *C. edwardii* and the larger *C. armbrusteri* are present. The association of these two canids seems to be typical only of late early Irvingtonian faunas, at least in Florida.

Specimens of *Smilodon gracilis* from Haile 21A are within the size range of the Leisey sample, but are smaller than specimens of *S. gracilis* from the middle Irvingtonian McLeod Limerock Mine (Berta 1987; this volume). The skeleton of a very large and apparently undescribed species of the sabercat *Homotherium* was recovered from Haile 21A. This large *Homotherium*, although very rare everywhere except Haile 21A, has also been recorded from three other early Irvingtonian faunas, Leisey, Inglis 1A, and Haile 16A. Besides Haile 21A, the

only other localities for *Desmodus archaeodaptes* are Inglis 1A and Haile 16A (Morgan et al. 1988; Morgan 1991). Haile 21A shares many diagnostic mammalian taxa with Leisey and likewise probably correlates with the latter part of the early Irvingtonian (1.6 and 1.0 Ma).

McLeod Limerock Mine.--The McLeod LF was recovered from the McLeod Limerock Mine located 3.3 km north of Williston, Levy County (Fig. 4, site 24). McLeod was excavated in 1941 by a Frick field party led by Ted Galusha, and the material from this site is now housed in the American Museum of Natural History. The fossils were recovered from a fine to coarse grayish clayey sand deposited in a solution feature in the marine Eocene Crystal River Formation. This site has long since been destroyed by mining operations (Frazier 1977).

No mammalian faunal list has been published for the McLeod LF. Fourteen diagnostic species of mammals known to be present in the McLeod LF are listed in Table 2, although this list is probably incomplete. The occurrence of *Smilodon gracilis* at McLeod indicates that this site is middle Irvingtonian or older (Berta 1987). The larger species *S. fatalis* (=*S. populator*) appears in the late Irvingtonian. *S. gracilis* specimens from McLeod are larger and more advanced than early Irvingtonian samples of this sabercat from Inglis 1A and Leisey Shell Pit, suggesting a younger age for McLeod (Berta 1987). The presence of *Tapirus haysii* also indicates a pre-late Irvingtonian age for McLeod, as this species is restricted to late early and middle Irvingtonian faunas in Florida (Hulbert this volume). The presence of *Canis armbrusteri* at McLeod rules out an earliest Irvingtonian age, as the oldest Florida records of this wolf is from the late early Irvingtonian Leisey Shell Pit. This canid survives until the late Irvingtonian where it is well represented at Coleman 2A (Martin 1974; Berta this volume). *Megalonyx wheatleyi*, represented at McLeod by a nearly complete skeleton (McDonald 1977), is most typical of middle Irvingtonian faunas, although it does occur in several Florida late early Irvingtonian sites.

One of the more diagnostic species present at McLeod is the extinct round-tailed muskrat, *Neofiber leonardi*. This species has been reported principally from late Irvingtonian faunas correlative with Coleman 2A (see below), including Rezabek (type locality) and Kanopolis in Kansas and Slaton in Texas (Frazier 1977). McLeod represents one of the earliest records of the large pampathere, *Holmesina septentrionalis*, a species that first appears in the middle Irvingtonian and survives until the end of the Pleistocene (Hulbert and Morgan 1993). One species from McLeod, *Neofiber leonardi*, appears to be restricted to the late Irvingtonian elsewhere, whereas two other species, *Smilodon gracilis* and *Tapirus haysii*, are otherwise unknown after the middle Irvingtonian. The Concurrent Range Zone of these three species in Florida constrains the age of McLeod to either late middle Irvingtonian or early late Irvingtonian, probably between 0.7 and 0.5 Ma.

Studies on mammals from the McLeod LF include Frazier (1977) on *Neofiber leonardi*, McDonald (1977) on *Megalonyx wheatleyi*, Edmund (1987) and Hulbert and Morgan (1993) on *Holmesina septentrionalis*, Berta (1987) on *Smilodon gracilis*, Berta (this volume) on *Canis armbrusteri*, Seymour (1993) on *Panthera onca*, and Emslie (this volume) on *Arctodus pristinus*.

Coleman 2A.--The Coleman 2A LF was collected from sands and clays deposited in a karst solution feature in the marine late Eocene Crystal River Formation in Sumter County in the north-central portion of the peninsula (Fig. 4, site 25). Like most other northern Florida karst deposits, the Coleman 2A Site was discovered in a commercial limestone mine and was subsequently destroyed by mining operations. Prior to Leisey, the Coleman 2A LF was the only Irvingtonian mammalian fauna from Florida to be studied comprehensively (Martin 1974).

Martin (1974:90) noted that the Coleman 2A LF, "...stands near the Irvingtonian-Rancholabrean boundary." He considered this fauna to be latest Irvingtonian in age because it lacks *Bison* and includes several taxa of mammals unknown from Florida Rancholabrean faunas. Coleman 2A is the only well known Florida vertebrate fauna that is late Irvingtonian in age. At least three species of mammals from Coleman 2A indicate an Irvingtonian age, *Arctodus pristinus*, *Canis armbrusteri*, and *Platygonus cumberlandensis*. *A. pristinus* occurs in most well sampled Florida Irvingtonian faunas, but is replaced in the Rancholabrean by the smaller tremarctine bear *Tremarctos floridanus*. *C. armbrusteri* ranges from the late early Irvingtonian through the late Irvingtonian, but is replaced in the early Rancholabrean by *C. dirus*. The large peccary *P. cumberlandensis* is known primarily from middle and late Irvingtonian faunas, although Martin (1974) also reported this species the early Rancholabrean Haile 7A LF. Wright (this volume) refers Florida early Irvingtonian *Platygonus* to the species, *P. vetus*, whereas Rancholabrean faunas are generally characterized by the smaller *P. compressus*.

Coleman 2A represents the oldest known record of two Rancholabrean (and living) species, *Didelphis virginiana* and *Neofiber alleni*. All other North American fossil occurrences of *D. virginiana* are from the Rancholabrean. The extinct muskrat *N. leonardi* occurs in several western faunas considered to be correlatives of Coleman 2A (Frazier 1977). The presence of *Didelphis* and *N. alleni* in Coleman 2A indicate a latest Irvingtonian age for this fauna. The tapir at Coleman 2A is *Tapirus veroensis*, the Rancholabrean species, and not *T. haysii* which is characteristic of late early and middle Irvingtonian faunas in Florida. Another link to the Rancholabrean is the cotton rat *Sigmodon bakeri*, originally described from Coleman 2A, but subsequently recognized from at least three Florida early Rancholabrean sites (Martin 1974). The large vole *Pitymys aratai* is presently known only from Coleman 2A (Martin 1974). Coleman 2A represents the oldest record of the Florida mouse, *Podomys floridanus*. The association of taxa restricted to the Irvingtonian (*Arctodus pristinus* and *Canis armbrusteri*) with

species typical of Rancholabrean faunas supports Martin's (1974) contention that Coleman 2A is latest Irvingtonian in age, probably between 0.5 and 0.3 Ma.

In addition to Martin's (1974) review of the entire mammalian fauna, other studies on mammals from Coleman 2A include Webb (1974b) on *Palaeolama*, Martin (1979) on *Sigmodon bakeri* (type locality), Frazier (1981) on *Erethizon dorsatum*, Wilkins (1984) on *Geomys pinetis*, Wilkins (1985) on *Thomomys orientalis*, Edmund (1987) on *Holmesina septentrionalis*, Seymour (1993) on *Panthera onca*, Emslie (this volume) on *Arctodus pristinus*, and Berta (this volume) on *Canis armbrusteri*. Ritchie (1980) reviewed the avifauna from Coleman 2A.

Other Florida Irvingtonian faunas.--Three additional Florida Irvingtonian faunas not included in Table 2 are worthy of mention. The Punta Gorda LF (Fig. 4, site 23) was collected in the banks of Alligator Creek near Punta Gorda, Charlotte County (Webb 1974a). The fossils were derived from a 1 m thick clay unit overlying marine shell beds tentatively referred to the Bermont Formation. Brooks (1968) provided a stratigraphic section for the Punta Gorda LF (="gomphothere site"). Punta Gorda was one of the first Irvingtonian sites reported from Florida (Webb 1974a), and was one of only four Irvingtonian faunas from the state mentioned by Kurtén and Anderson (1980). Webb (1974a) listed the mammalian fauna from Punta Gorda which is composed of only nine species. The most abundant mammals in the Punta Gorda LF are the proboscideans *Mammuthus hayi* and *Cuvieronius tropicus*. The mammoth from this site is very similar to *M. hayi* reported from Leisey (Webb and Dudley this volume). Although the presence of *Cuvieronius* at Punta Gorda was originally thought to indicate an early Pleistocene age, this last North American gomphothere is now known to have survived into the early Rancholabrean in Florida. Other Irvingtonian taxa present at Punta Gorda include *Equus "leidyi"* and *Holmesina floridanus*. The age of the Punta Gorda LF is not entirely clear because of the depauperate fauna, particularly the lack of carnivores and rodents, but there are several constraints on its age. The presence of mammoth confirms that this site is younger than 1.6 Ma, thus ruling out an earliest Irvingtonian age. A late early Irvingtonian age for Punta Gorda is most probable owing to the similarity between the mammoths from this site and Leisey.

A mixed assemblage of Irvingtonian and Rancholabrean vertebrates has been recovered from Apollo Beach in Hillsborough County, just north of the Leisey Shell Pit (Fig. 4, site 18). Mammals in the Apollo Beach fauna that are shared with Leisey include *Castoroides*, *Neochoerus*, *Erethizon dorsatum*, *Arctodus pristinus*, *Tapirus haysii*, and an undescribed species of *Equus* (*Hemionus*). The Apollo Beach LF is probably late early Irvingtonian in age.

Waldrop and Wilson (1990) reported *Canis edwardii* and *Chasmaporthetes ossifragus* from a unit underlying the Caloosahatchee Formation in the Forsberg

Shell Pit, near Punta Gorda in Charlotte County (Fig. 4, site 14). These same two carnivores also occur together in the Inglis 1A and De Soto Shell Pit faunas. *Chasmaporthetes* is known from both late Blancan and earliest Irvingtonian faunas in Florida, whereas *Canis edwardii* is restricted to the early Irvingtonian. Three additional mammalian taxa, *Pachyarmatherium leiseyi*, an intermediate-sized *Holmesina floridanus*, and *Smilodon gracilis*, have been collected recently from within shell beds of the Caloosahatchee Formation at the Forsberg Shell Pit. This represents the first well-documented earliest Irvingtonian record of *P. leiseyi*. The stage of evolution of the *Holmesina* from the Forsberg Shell Pit is typical of other early Irvingtonian faunas such as Inglis 1A, Haile 16A, and Leisey Shell Pit. *Smilodon gracilis* is found from the late Blancan through the middle Irvingtonian in Florida. Most of the mammalian taxa from the Forsberg Shell Pit LF are indicative of an early Irvingtonian age. The Concurrent Range Zone of *Canis edwardii* and *Chasmaporthetes ossifragus* further constrains the age as earliest Irvingtonian, between 2.0 and 1.6 Ma.

RANCHOLABREAN

Webb (1974a) provided mammalian faunal lists for more than 30 Rancholabrean sites from Florida and Kurtén and Anderson (1980) discussed many of these same sites as well. Rancholabrean vertebrate faunas are not treated separately in our discussion or in Table 2. We have combined a number of the best known sites to compile composite faunal lists for both the early Rancholabrean and late Rancholabrean (Table 2). The composite Rancholabrean faunal lists are important to our discussion because they extend the chronological distribution of late Pliocene and early to middle Pleistocene mammals to include the late Pleistocene and Holocene. We briefly summarize our criteria for recognizing Rancholabrean faunas in Florida, and for distinguishing between the early and late Rancholabrean.

The first appearance of *Bison* in North America at about 300 ka is generally used to define the base of the Rancholabrean NALMA (Savage 1951; Lundelius et al. 1987). The boundary between the early and late Rancholabrean corresponds to the beginning of the last or Sangamonian interglacial at about 130 ka. Although the presence of *Bison* is convenient for defining the Rancholabrean, this genus is often absent in Florida Rancholabrean faunas. Therefore, it has been necessary to establish other faunal criteria for recognizing Rancholabrean faunas.

Didelphis virginiana was long to thought to be restricted to Rancholabrean and modern faunas. However, Martin (1974) reported *Didelphis* from the latest Irvingtonian Coleman 2A fauna. Both the glyptodont *Glyptotherium floridanum* and the ground sloth *Megalonyx jeffersonii* are known only from Rancholabrean

faunas in Florida (McDonald 1977; Kurtén and Anderson 1980; Gillette and Ray 1981). The dire wolf, *Canis dirus*, is restricted to Rancholabrean faunas in North America (Kurtén and Anderson 1980). *C. dirus* is one of the most common large carnivores in Florida Rancholabrean faunas. The Florida cave bear, *Tremarctos floridanus*, also is found only in Rancholabrean faunas in Florida. The larger tremarctine, *Arctodus pristinus*, is the characteristic bear of late Blancan and Irvingtonian faunas in the state. Although the largest and best known North American species of *Smilodon*, *S. fatalis* (=*S. populator* of Berta 1985), first appears in the late Irvingtonian (Kurtén and Anderson 1980), it is not recorded from Florida until the early Rancholabrean. The rice rat, *Oryzomys palustris*, is unknown in Florida or elsewhere in the United States prior to the Rancholabrean. Neotropical oryzomyine rodents ultimately were derived from North America during the Pliocene (Baskin 1986), but the genus *Oryzomys* apparently evolved either in South America or tropical North America and then reinvaded temperate North America in the late Pleistocene. *Didelphis virginiana*, *Oryzomys palustris*, and *Dasypus novemcinctus* were the last Neotropical mammals to reach the United States as participants in the Great American Interchange.

The presence of the giant bison, *Bison latifrons*, is often used to identify early Rancholabrean faunas (Robertson 1974; Kurtén and Anderson 1980). Despite the supposed occurrence of *B. latifrons* in several Wisconsinan faunas in western North America, the two richest samples of this species in Florida, Bradenton LF and Haile 8A (Robertson 1974), are in faunas known to be early Rancholabrean in age based on other taxa. The gomphothere *Cuvieronius tropicus* also appears to have gone extinct in Florida during the early Rancholabrean, with the youngest record from the early Rancholabrean Daytona Beach LF. Although there are no published late Rancholabrean records of the giant ground sloth *Eremotherium* from Florida, several fragamentary specimens of *E. mirabile* have been identified recently from the late Rancholabrean Vero and Oklawaha River faunas. The vole, *Pitymys hibbardi*, originally described from the early Rancholabrean Williston 3A LF (Holman 1959) and since identified from the Bradenton and Haile 7A faunas (Martin 1974), appears to be restricted to the early Rancholabrean in Florida. The extinct cotton rat, *Sigmodon bakeri*, described from the late Irvingtonian Coleman 2A LF (Martin 1974), is known from the same three early Rancholabrean localities as is *P. hibbardi*.

The late Rancholabrean comprises the time interval from about 130 to 10 ka, including the last or Sangamonian interglacial (ca. 130 to 120 ka) and the last or Wisconsinan glacial (120 to 10 ka). The latter half of the late Rancholabrean (<50 ka) is within the range of radiocarbon dating, and as a result a very detailed chronology is known for this time period. Because of its proximity to the Recent, there are far more late Rancholabrean vertebrate faunas known in North America than from any other age. This is also true for Florida where there are more than 100 late Rancholabrean faunas. The composite list of Florida late Rancholabrean

mammals in Table 2 is derived from the faunal lists of the eight most prolific faunas of this age (faunas listed in footnote to Table 2). See Webb (1974a) and Webb and Wilkins (1984) for individual faunal lists for the best known Florida late Rancholabrean mammalian faunas.

Several species of Florida Pleistocene mammals are restricted to late Rancholabrean faunas. The American lion *Panthera atrox* (=*P. leo atrox* of Kurtén and Anderson 1980) is a Rancholabrean immigrant from the Old World. In Florida, *P. atrox* is known only from late Rancholabrean faunas. Florida's only surviving large cat, the puma or Florida panther, *Puma concolor*, first appears in the state during the late Rancholabrean, as does *Bison antiquus* (Robertson 1974). Four species of rodents, *Sciurus niger*, *Pitymys pinetorum*, *Microtus pennsylvanicus*, and *Ondatra zibethicus*, are restricted to Florida late Rancholabrean faunas, although the latter two species occur in older faunas elsewhere (Martin 1974; Kurtén and Anderson 1980). The extant cotton rat *Sigmodon hispidus* is typical of Florida late Rancholabrean faunas (Martin 1974 1979), although the earliest appearance of this species is in the late early Rancholabrean Daytona Beach and Haile 8A local faunas. The end of the Pleistocene is marked by the appearance of humans about 12 ka and the subsequent extinction of the mammalian megafauna by about 10 ka, as well as the return to interglacial conditions with a rise in sea level to its present position.

SUMMARY

Vertebrate fossils of four different ages have been recovered from the Leisey Shell Pit in southwestern Hillsborough County, Florida. In ascending stratigraphic/chronologic order these are: Arcadia Formation (late early or early middle Miocene); Bone Valley Formation or stratigraphic equivalent (late Miocene); Bermont Formation (early Pleistocene); and Fort Thompson Formation (late Pleistocene). The Bermont Formation at Leisey consists of massive, sandy, marine shell beds, with occasional lenses of dark, organic-rich silt and fine-grained sand. These lenses produce the Leisey Shell Pit Local Fauna, a diverse, late early Irvingtonian (1.6-1.0 Ma) vertebrate assemblage composed of over 200 taxa.

The age of the Leisey Shell Pit LF has been determined primarily by vertebrate biochronology, with corroboration from paleomagnetic polarity and strontium isotope chronology. Many types of biochronologic information are used, including first occurrences of immigrant taxa; first occurrences of species that evolved in situ; concurrent or overlapping range zones; stage of evolution in morphologically-changing lineages; and last occurrences of key taxa that presumably represent extinction. The latter must be used with caution as there are many other reasons a taxon may be absent from a fauna. Although broadly similar

to other regions of North America, fossil vertebrates from Florida include some endemic elements and a diverse fauna of Neotropical immigrants, as well as differences in timing of first and last occurrences.

Dating marine shell beds using interbedded terrestrial vertebrate faunas has long been applied in Florida, but not always successfully due to inadequate faunas and the limited understanding of mammalian biochronology in the state prior to the last 20 years. Both of these problems have been rectified with recent discoveries of rich land mammal faunas from southern Florida, particularly the late Blancan Macasphalt Shell Pit LF, the earliest Irvingtonian De Soto Shell Pit LF, and of course, Leisey Shell Pit. Our work suggests that the Pinecrest Beds are late Pliocene (2.5-2.0 Ma), the Caloosahatchee Formation is latest Pliocene (2.0-1.6 Ma), and the Bermont Formation is early Pleistocene (1.6-1.0 Ma). Previous interpretations of the age of the Bermont ranged from late Pliocene to middle Pleistocene. Results from vertebrate biochronology are consistent with those from paleomagnetic polarity (reversed, Matuyama Chron) and broadly concordant with strontium isotope chronology. However, the numerical dates from the strontium isotope ratios are older than those based on vertebrate biochronology, ranging into the late Pliocene. Combining age criteria from all of these sources, as well as sea-level evidence, results in a most likely chronologic range for the Leisey Shell Pit LF of 1.5 to 1.1 Ma, or late early Irvingtonian.

Among vertebrate faunas outside of Florida, the Leisey Shell Pit LF shares the most taxa with the early Irvingtonian Gilliland LF in Texas. The correlative Holloman LF of Oklahoma is also very similar. Leisey is older than the two best known middle Irvingtonian faunas from eastern North America, Cumberland Cave, Maryland and Port Kennedy Cave, Pennsylvania.

Biochronologic analysis of Florida vertebrate faunas results in the recognition of eight distinct assemblages from the late Pliocene through the end of the Pleistocene. These predominantly mammalian assemblages should be useful for correlation within Florida and elsewhere in the southeastern United States. Age ranges for the eight Florida vertebrate assemblages listed below are approximate, but should be accurate to within about ±0.2 Ma.

1. **Late Blancan** (2.5-2.0 Ma). Characterized by the limited occurrence of *"Glossotherium" chapadmalense*, *Borophagus diversidens*, *Canis lepophagus*, *Sigmodon medius*, *Nannippus peninsulatus*, *Equus* (*Dolichohippus*) sp., *Platygonus bicalcaratus*, *Hemiauchenia blancoensis*, and *Rhynchotherium praecursor*. First occurrence of Neotropical immigrant genera that participated in the Great American Interchange, including *Dasypus*, *Holmesina*, *Glyptotherium*, *Pachyarmatherium*, *"Glossotherium,"* *Eremotherium*, and *Titanis*. Only Florida Plio-Pleistocene vertebrate assemblage characterized by the overlapping range zone of *Nannippus* and these Neotropical immigrants. Best exemplified

by the Santa Fe River 1, Macasphalt Shell Pit, Haile 15A, and Kissimmee River local faunas.

2. **Latest Blancan** (ca. 2.0 Ma). This is probably the most poorly defined of the Florida Plio-Pleistocene vertebrate assemblages, as the single fauna representing this time interval has yet to be fully described. Characterized by the first well-documented occurrences of new species of *Eremotherium* and *Tapirus*; by the first occurrence of *Erethizon* and *Neotoma*; and by the last occurrence of a large, undescribed species of *Chelydra*. The *Holmesina floridanus* sample from this assemblage is intermediate in size between the very small form from the late Blancan and the larger form from the earliest Irvingtonian. Only known by the Haile 7C LF.

3. **Earliest Irvingtonian** (2.0-1.6 Ma). Characterized by the limited occurrence of *Erethizon kleini*, *Sigmodon curtisi*, *Ondatra idahoensis*, and an undescribed dwarf species of *Hemiauchenia*; and by the first occurrence of *Paramylodon harlani*, *Canis edwardii*, *Lepus* sp., *Equus "leidyi,"* and *Mammut americanum*. Taxa shared with the late Blancan assemblage but absent in succeeding faunas include *Megalonyx leptostomus*, *Trigonictis macrodon*, *Chasmaporthetes ossifragus*, and *Capromeryx arizonensis*, as well as the emydid turtle *Trachemys platymarginata* and the giant phororhacid bird *Titanis walleri*. Best exemplified by the Inglis 1A and De Soto Shell Pit local faunas.

4. **Late early Irvingtonian** (1.6-1.0 Ma). Characterized by the limited occurrence of *Nothrotheriops texanus*, *Ondatra annectens*, and *Mammuthus hayi*; the first occurrences of *Megalonyx wheatleyi*, *Canis armbrusteri*, *Lutra canadensis*, *Castoroides*, *Erethizon dorsatum*, *Geomys pinetis*, *Podomys*, *Sigmodon libitinus*, *Pedomys*, *Synaptomys*, *Sylvilagus floridanus*, *Sylvilagus palustris*, *Tapirus haysii*, *Palaeolama mirifica*, and the emydid turtle *Trachemys scripta*; and the last occurrence of *Glyptotherium arizonae*, *Pachyarmatherium leiseyi*, *Canis edwardii*, *Trigonictis*, *Geomys propinetis*, and *Sylvilagus webbi*. Best exemplified by the Haile 16A, Leisey Shell Pit, Pool Branch, Payne Creek Mine, Crystal River Power Plant, and Haile 21A local faunas.

5. **Middle Irvingtonian** (1.0-0.6 Ma). Characterized by the presence of *Neofiber leonardi* and an advanced grade of *Smilodon gracilis*; by the first occurrence of *Holmesina septentrionalis*, *Panthera onca*, and *Sigmodon bakeri*; and by the last occurrence of *Megalonyx wheatleyi*, *Smilodon gracilis*, and *Tapirus haysii*. Only known by the McLeod LF which probably falls late in the interval.

6. **Late Irvingtonian** (0.6-0.3 Ma). Characterized by the limited occurrence of *Urocyon minicephalus* and *Pitymys aratai*; by the first occurrence of *Didelphis virginiana*, *Procyon lotor*, *Thomomys orientalis*, *Podomys floridanus*, *Neofiber alleni*, and *Tapirus veroensis*; and by the

last occurrence of *Arctodus pristinus* and *Canis armbrusteri*. Represented only by the Coleman 2A LF which is very late in the interval.

7. **Early Rancholabrean** (0.3 Ma-130 ka). Characterized by the limited occurrence of *Bison latifrons* and *Pitymys hibbardi*; by the first occurrence of *Glyptotherium floridanum*, *Megalonyx jeffersonii*, *Canis dirus*, *Tremarctos floridanus*, *Smilodon fatalis*, *Oryzomys palustris*, *Sigmodon hispidus*, *Synaptomys australis*, *Platygonus compressus*, and *Mammuthus columbi*; and by the last occurrence of *Cuvieronius* and *Sigmodon bakeri*. Best exemplified by the Bradenton, Daytona Beach, Haile 7A, Oldsmar, and Williston 3A local faunas.

8. **Late Rancholabrean** (130-10 ka). Characterized by the limited occurrence of *Panthera atrox*, *Dinobastis serus*, and *Bison antiquus*; by the first occurrence of *Sciurus niger*, *Pitymys pinetorum*, *Microtus pennsylvanicus*, *Ondatra zibethicus*, and *Puma concolor*; and by the last local occurrence of numerous genera at the end of the interval. These include *Holmesina*, *Glyptotherium*, *Eremotherium*, *Megalonyx*, *Paramylodon*, *Desmodus*, *Conepatus*, *Smilodon*, *Panthera*, *Tremarctos*, *Castoroides*, *Neochoerus*, *Mylohyus*, *Platygonus*, *Hemiauchenia*, *Palaeolama*, *Equus*, *Tapirus*, *Mammut*, and *Mammuthus*. Among the more than 100 late Rancholabrean faunas from Florida the best known are Arredondo 2A, Cutler Hammock, Devils Den, Ichetucknee River, Melbourne, Monkey Jungle Hammock, Reddick 1, Seminole Field, and Vero.

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