

SMALL MAMMALS (INSECTIVORA, LAGOMORPHA, AND RODENTIA) FROM THE EARLY PLEISTOCENE (IRVINGTONIAN) LEISEY SHELL PIT LOCAL FAUNA, HILLSBOROUGH COUNTY, FLORIDA

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ABSTRACT

Twelve species of small mammals, including one species of Insectivora, two species of Lagomorpha, and nine species of Rodentia, are reported from the early Pleistocene (early Irvingtonian) Leisey Shell Pit Local Fauna, Hillsborough County, Florida. Most taxa of small mammals are rare in the Leisey fauna. The most common species is the sigmodontine rodent *Sigmodon libitinus*, followed in abundance by the hydrochaerid *Neochoerus* sp., the arvicoline *Pedomys* sp., the soricid *Blarina* cf. *B. carolinensis*, the geomyid *Geomys pinetis*, the giant castorid *Castoroides leiseyorum*, the erethizontid *Erethizon dorsatum*, and the leporid *Sylvilagus floridanus*. Four undescribed species of rodents occur at Leisey, three of which, the arvicolines *Pedomys* and *Synaptomys* sp. and the large peromyscine *Podomys* sp., are represented by insufficient material for formal description. *Castoroides leiseyorum* is described as a new species that differs from the Rancholabrean *C. ohioensis* in the absence of a mesopterygoid fossa, but is similar to the latter in size and most other morphological characters. Biochronological analysis of the rodents and lagomorphs from Leisey indicates a late early Irvingtonian age, probably between 1.3 and 1.0 Ma. *C. leiseyorum*, *S. libitinus*, and the undescribed species of *Pedomys*, *Synaptomys*, and *Podomys* are known only from Florida late early Irvingtonian faunas. The records of *S. floridanus*, *G. pinetis*, and *E. dorsatum* from Leisey are among the oldest occurrences of these extant species. Other Florida small mammal faunas similar in age to Leisey are Haile 16A, Haile 21A, and Payne Creek Mine. Correlative early Irvingtonian faunas from western North America include: Gilliland, Texas; Holloman, Oklahoma; Kentuck and Wathena, Kansas; Sappa, Nebraska; and Java, South Dakota.

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RESUMEN

Desde la fauna local del depósito de conchuelas de Leisey, condado de Hillsborough, Florida, se reportan doce especies de mamíferos pequeños, incluyendo una especie del orden Insectivora, dos especies de Lagomorpha y nueve especies de Rodentia provenientes del Pleistoceno temprano (Irvingtoniano temprano). La mayoría de los taxones de pequeños mamíferos son raros en la fauna de Leisey. La especie más común es el roedor sigmodóntido *Sigmodon libitinus*, seguido en abundancia por el hydrochaerido *Nechoerus* sp., el arvicolino *Pedomys* sp., el soricido *Blarina* cf. *B. carolinensis*, el geomyo *Geomys pinetis*, el castorido gigante *Castoroides leiseyorum*, el erethizóntido *Erethizon dorsatum*, y el lepórido *Sylvilagus floridanus*. En Leisey existen cuatro especies de roedores no descritos, tres de los cuales, los arvicolinos *Pedomys* y *Synaptomys* sp. y el gran peromyscino *Podomys* sp., se encuentran representados por insuficiente material como para permitir una adecuada descripción. *Castoroides leiseyorum* se describe como una nueva especie que difiere del Rancholabreano *C. ohioensis* por carecer de una fosa mesopteigoidea, aún cuando se asemeja a la primera en tamaño y en la mayoría de los caracteres morfológicos. Análisis biocronológicos de roedores y lagomorfos provenientes de Leisey indican una edad Irvingtoniana temprana tardía, probablemente de entre 1.3 y 1.0 Ma. *C. leiseyorum*, *S. libitinus*, y la especie no descrita de *Pedomys*, *Synaptomys* y *Podomys* se conocen desde faunas Irvingtonianas tempranas tardías en Florida. Los registros de *S. floridanus*, *G. pinetis* y *E. dorsatum* provenientes de Leisey se encuentran dentro de los más antiguos para estas especies actualmente existentes. Otras faunas de pequeños mamíferos de Florida similares en edad a Leisey son Haile 16A, Haile 21A y la Mina Payne Creek. Las siguientes son faunas correlativas al Irvingtoniano temprano del oeste de Norte América: Gilliland, Texas; Holloman, Oklahoma; Kentuck y Wathena, Kansas; Sappa, Nebraska; y Java, Dakota del Sur.

INTRODUCTION

The small mammal fauna from the Leisey Shell Pit is composed of 12 species belonging to the orders Insectivora, Lagomorpha, and Rodentia. The term "small mammals" as used here refers to those orders of mammals typically consisting of species of small body size, although two of the rodents in the Leisey fauna are hardly small. The giant beaver *Castoroides* was bear-sized by some estimates and the extinct capybara *Nechoerus* was larger than the largest living rodent, the capybara *Hydrochaeris*. The remainder of the small mammals in the Leisey Shell Pit LF are indeed small in body size (less than 5 kg). Two other orders of small mammals commonly found in Florida Pleistocene vertebrate faunas, the Chiroptera and Marsupialia, are absent from Leisey.

The Leisey Shell Pit Local Fauna (LF) includes vertebrate fossils collected from early Pleistocene sediments of the Bermont Formation in two large, nearly contiguous shell pits located less than 1 km inland from Tampa Bay about 7 km southwest of Ruskin, Hillsborough County, Florida. These two shell pits, owned by the Leisey Shell Corporation, were designated Leisey 1 and Leisey 3 by Hulbert and Morgan (1989). Specific collecting localities within the Leisey pits are designated by letters (e.g. Leisey 1A, Leisey 3A, etc.). A third pit, Leisey 2, contains primarily Rancholabrean vertebrates and is thus excluded from this analysis. Hulbert and Morgan (1989) and Morgan and Hulbert (this volume)

provided maps, coordinates, stratigraphic sections, and other information for the individual Leisey Shell Pit sites. These two papers should be consulted for more detailed geologic and geographic data.

Small mammals are one of the most poorly represented groups of vertebrates in the Leisey Shell Pit LF. The Leisey small mammal fauna includes one species of insectivore, two lagomorphs, and nine rodents. Both the species diversity and abundance of small mammals at Leisey are low compared to several other well known Florida Irvingtonian sites. The most abundant species, the extinct cotton rat *Sigmodon libitinus*, is represented by more than 50 specimens. However, half of the species of small mammals from Leisey are known from fewer than five specimens. Of the two richest Leisey Shell Pit localities, Leisey 1A and Leisey 3A, the largest sample of microvertebrates is from Leisey 3A. Leisey 1A yielded remarkable samples of ungulates, ground sloths, and large carnivores, but few terrestrial microvertebrates (Hulbert and Morgan 1989; Webb et al. 1989). The rarity of small mammals in the Leisey Shell Pit LF is not primarily a result of collecting bias since field crews from the Florida Museum of Natural History screenwashed and sorted over 1 metric ton of matrix from the bone-bearing layers in the Leisey 1A and 3A sites. The hypothesized shallow marine or estuarine depositional environment and accompanying taphonomic factors apparently had an adverse affect on the sampling and preservation of small mammals in the Leisey sites (Pratt and Hulbert this volume). Other small terrestrial vertebrates such as lizards, snakes, and passerine birds are also uncommon in the Leisey Shell Pit LF (see papers by Meylan and Emslie elsewhere in this volume).

Florida has a wealth of Irvingtonian vertebrate faunas (Morgan and Hulbert this volume), but only a few of these have been thoroughly analyzed. The three best known Irvingtonian vertebrate faunas from Florida prior to the discovery of Leisey are all rich in small mammals, including the earliest Irvingtonian Inglis 1A LF in Citrus County (Webb 1974; Kurtén and Anderson 1980; Webb and Wilkins 1984; Morgan 1991), the early Irvingtonian Haile 16A LF in Alachua County (Ray et al. 1981; Morgan et al. 1988; Morgan 1991), and the late Irvingtonian Coleman 2A LF in Sumter County (Martin 1974; Kurtén and Anderson 1980). These three faunas occur as cave or fissure fillings in the extensive karst terrain of northern peninsular Florida. Morgan and Hulbert (this volume) provide synopses of the mammalian faunas from Inglis 1A, Haile 16A, and Coleman 2A, including both large and small mammals. With the exception of Martin's (1974) comprehensive analysis of the Coleman 2A LF and a preliminary faunal list for Inglis 1A (Webb and Wilkins 1984), most previous studies on Florida Irvingtonian small mammals have consisted of reviews of selected taxonomic groups. The abundant insectivores, lagomorphs, and rodents in the Inglis 1A, Haile 16A, and Coleman 2A sites are very useful for purposes of comparison with the more limited micromammal fauna from Leisey.

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METHODS AND ABBREVIATIONS

Responsibility for the three orders of small mammals from Leisey was divided between the authors, with GSM covering the Insectivora and Rodentia and JAW writing the section on Lagomorpha. Measurements are in mm and were taken with either dial calipers (accurate to 0.1 mm) or a Gaertner measuring microscope (accurate to 0.01). All Leisey specimens described here are housed in the Vertebrate Paleontology Collection of the Florida Museum of Natural History, University of Florida, Gainesville. More complete information on the various fossil localities discussed in the text, including field notes, detailed map data, photographs, etc. are available in the vertebrate paleontology locality files of the Florida Museum of Natural History.

Abbreviations used in the text are as follows:

UF	Florida Museum of Natural History, University of Florida (formerly the Florida State Museum)
LF	Local Fauna
NALMA	North American Land Mammal Age
Ma	Mega-anna=millions of years before present
ka	kilo-anna=thousands of years before present
MNI	Minimum number of individuals
P/p	Upper/lower premolar (e.g. P4 is the fourth upper premolar)
M/m	Upper/lower molar (e.g. m1 is the first lower molar)

CHRONOLOGY

Because we discuss the biochronology of the small mammals from Leisey and other Florida Irvingtonian sites in some detail, the chronology of the Pleistocene Epoch and the Irvingtonian Land Mammal Age are briefly summarized (see more extensive discussion in Morgan and Hulbert this volume). The boundaries and subdivisions of the Pleistocene follow Berggren et al. (1985) and Harland et al.

(1990). The Pliocene/Pleistocene boundary is placed at 1.64 Ma, slightly above the top of the Olduvai Normal Subchron of the Matuyama Chron. The Pleistocene is subdivided into the early, middle, and late Pleistocene. 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 Pleistocene covers the interval from the beginning of the Brunhes Chron at 0.78 Ma until the onset of the last (Sangamonian) interglacial at 130 ka. The late Pleistocene covers the period between 130 and 10 ka.

The late Pliocene and Pleistocene incorporate three North American Land Mammal Ages: Blancan, Irvingtonian, and Rancholabrean. We follow the definitions and subdivisions of these three NALMA proposed by Lundelius et al. (1987). The Leisey Shell Pit LF is Irvingtonian in age and accordingly this NALMA will be our primary focus; however, we also discuss taxa of small mammals from the late Blancan and Rancholabrean. The Blancan/Irvingtonian boundary is placed at about 1.9 Ma, while the Irvingtonian/Rancholabrean boundary is about 0.3 Ma. The Blancan is entirely within the Pliocene covering the time period from 4.5 to 1.9 Ma. Early and middle Blancan land mammal faunas are unknown from Florida. Two late Blancan sites (between 2.5 and 1.9 Ma) containing small mammals have been reported from the state, the Haile 15A LF in Alachua County (Robertson 1976) and the Macasphalt Shell Pit LF in Sarasota County (Morgan and Ridgway 1987).

The Irvingtonian covers the latest Pliocene and much of the Pleistocene (between 1.9 and 0.3 Ma), and therefore it is useful to subdivide this NALMA into smaller units. Lundelius et al. (1987) recognized three subages of the Irvingtonian: early Irvingtonian (Sappan), middle Irvingtonian (Cudahyan), and late Irvingtonian (Sheridanian). The boundaries between the three Irvingtonian subdivisions are not well defined, but their approximate age ranges are as follows: early Irvingtonian (1.9-1.0 Ma); middle Irvingtonian (1.0-0.6 Ma); late Irvingtonian (0.6-0.3 Ma). The early Irvingtonian covers nearly a million years and transcends the Pliocene-Pleistocene boundary. Accordingly, this time period is informally subdivided into the earliest Irvingtonian (1.9-1.6 Ma, latest Pliocene) and the late early Irvingtonian (1.6-1.0 Ma, early Pleistocene). The Rancholabrean begins about 300 ka and ends at the Pleistocene/Holocene boundary at 10 ka. The boundary between the early Rancholabrean (300 ka-130 ka) and the late Rancholabrean (130-10 ka) approximates the beginning of the last (Sangamonian) interglacial high sea level stand.

Repenning (1980; 1987) and L. D. Martin (1979) both proposed biochronologies for the Blancan through the Rancholabrean NALMA based on evolutionary stages and immigration events of arvicoline or microtine rodents. The Irvingtonian I and Irvingtonian II of Repenning (1987) are more or less equivalent to the early and middle Irvingtonian, respectively, as defined above. However, the Rancholabrean I of Repenning (1987), is essentially the same as the late Irvingtonian recognized here and by Lundelius et al. (1987).

A mammalian biochronology that uses many different taxa of both small and large mammals (e.g. Lundelius et al. 1987) is more applicable to Florida Plio-Pleistocene faunas than a scheme based solely on arvicoline rodents, which are generally rare in Florida. Many species of mammals characteristic of western and Appalachian Irvingtonian sites are absent from Florida, whereas many Florida Irvingtonian mammals are unknown from faunas outside the state. Martin (1974, fig. 3.17) presented a chart showing the temporal distribution of selected Florida Plio-Pleistocene mammals, including both small and large taxa. Based on data from many new sites, Morgan and Hulbert (this volume) compiled a comprehensive biochronology of Florida Plio-Pleistocene mammals. A synopsis of their biochronology concentrating on Irvingtonian small mammals is provided in the Discussion section.

SYSTEMATIC PALEONTOLOGY

Order INSECTIVORA Bowdich 1821

Family SORICIDAE Gray 1821

Blarina cf. *B. carolinensis* (Bachman 1837)

Referred Specimens.—Leisey 3A: UF 124335, left mandible with m1; UF 124336, edentulous left mandible; UF 132069, posterior half of edentulous left mandible. MNI=3.

Description.—Three fragmentary mandibles are the only specimens of insectivores from the Leisey Shell Pit LF. All three mandibles are considerably larger than the least shrew, *Cryptotis parva*, and are similar in size to modern mandibles of the short-tailed shrew, *Blarina carolinensis*, from the Florida peninsula. The single soricid m1 from Leisey (UF 124335) is also similar in morphological characters and size (Table 1) to modern and fossil Florida specimens of *B. carolinensis*. However, two slight differences were noted; the Leisey m1 seems to have a somewhat more anteroposteriorly compressed talonid basin and the entoconid is more posteriorly placed.

Table 1 includes m1 measurements (total length and trigonid length) of one Blancan, four Irvingtonian, and two extant samples of *Blarina* from Florida. The modern samples include two subspecies, *B. c. carolinensis* from Citrus County in the northern half of the Florida peninsula and *B. carolinensis peninsulae* from Highlands County in the southern peninsula. Irvingtonian *Blarina* samples consist of specimens from the earliest Irvingtonian Inglis 1A LF, the early Irvingtonian Haile 16A LF, Leisey Shell Pit, and the late Irvingtonian Coleman 2A LF. Jones et al. (1984) examined and measured the fossil *Blarina* mandibles from Inglis 1A and

Table 1. Dental measurements (in mm) of Blancan, Irvingtonian, and modern *Blarina* from Florida. Mean, observed range, and sample size, respectively, are provided for samples larger than one individual.

Locality	Age	Length of m1	Length of m1 trigonid
Haile 15A <i>cf. Blarina</i> UF 17466	late Blancan	1.5	1.0
Inglis 1A <i>B. cf. B. carolinensis</i>	earliest Irvingtonian	1.8 1.7-1.9 N=5	1.2 1.2 N=5
Haile 16A <i>B. cf. B. carolinensis</i>	early Irvingtonian	1.6 1.5-1.7 N=11	1.0 0.9-1.1 N=11
Leisey 3A <i>B. cf. B. carolinensis</i> UF 124335	early Irvingtonian	1.55	1.0
Coleman 2A <i>B. cf. B. carolinensis</i> UF 11626	late Irvingtonian	1.8	1.2
Citrus County <i>B. c. carolinensis</i>	Recent	1.6 1.5-1.7 N=10	1.0 0.9-1.1 N=10
Highlands County <i>B. c. peninsulae</i>	Recent	1.7 1.6-1.8 N=10	1.1 1.0-1.2 N=10

Coleman 2A, both of which they referred to *B. carolinensis*. The three Leisey shrew mandibles, and in particular the m1 (UF 124335), are virtually identical in size and morphological features to the sample of *Blarina* from Haile 16A. The m1s from Leisey and Haile 16A are within the range of *B. c. carolinensis* from northern Florida (Table 1). The Leisey shrews are tentatively referred to *B. carolinensis* based on their overall similarity in morphology and size to modern Florida samples of that species. The Inglis and Coleman *Blarina*, as well as extant *B. carolinensis peninsulae*, are larger than the Leisey specimens.

Remarks.—Until recently almost all extant *Blarina* from eastern North America were placed in the species *B. brevicauda*. Jones et al. (1984) demonstrated that *B. brevicauda* actually consists of at least three different species. *B. carolinensis* is the living representative of this genus in the southeastern United States. Jones et al. (1984) provided measurements of a large series of *Blarina* from throughout eastern North America which showed that *B. carolinensis peninsulae* from southern peninsular Florida is the smallest living subspecies of North American *Blarina*. However, our measurements of a sample of *B. c. carolinensis* from Citrus County in northern Florida averaged slightly smaller than a sample of *B. c. peninsulae* from Highlands County in southern Florida (Table 1). Despite these slight inconsistencies, the overall small size of Florida *B. carolinensis* is clearly established.

The systematics of the late Blancan and Irvingtonian shrews from Florida cannot be properly addressed here, owing to the fragmentary condition of the three Leisey soricid specimens. Robertson (1976) reported a mandible of *Cryptotis parva* (UF 17466) from the late Blancan Haile 15A LF in Alachua County. He stated that this specimen was indistinguishable from modern Florida specimens of *C. parva*, except for its slightly larger size. However, the Haile 15A shrew has an unreduced talonid on m3, a character of *Blarina* (Repenning 1967), and the m1 is similar in size to m1s of extant *B. carolinensis* and fossils from Leisey and Haile 16A (see Table 1). The key to understanding the evolutionary history of Florida Plio-Pleistocene shrews lies in a detailed analysis of the large soricid samples from Inglis 1A and Haile 16A, both of which possess a small and a large species.

Other early Irvingtonian records of *B. carolinensis*, in addition to those from Florida, include specimens from Wathena, Kansas and Java, South Dakota. Both of these localities are outside the present range of this species (Jones et al. 1984). Middle Irvingtonian records of *B. carolinensis* from Cumberland Cave, Maryland and Hanover Quarry, Pennsylvania are also well outside the current southeastern range of *B. carolinensis*.

Order LAGOMORPHA Brandt 1855

Family LEPORIDAE Gray 1821

Sylvilagus floridanus (Allen 1890)

Referred Specimens.—Leisey 3A: UF 96220, partial right mandible with p3; UF 96221, left p3. MNI=1.

Tentatively Referred Specimens.—Leisey 1A: UF 83120, right and left premaxillae with left I1 and right I2; UF 131997, right I1; UF 87965, two associated upper cheek teeth; UF 131996, upper cheek tooth; UF 131995, associated left I1 and two upper cheek teeth; UF 86229, scapula; UF 88035, 131994, distal humeri (2); UF 87966, proximal radius; UF 87963, proximal ulna;

UF 81131, distal tibia; UF 85320, calcaneum; Leisey 3: UF 102666, distal humerus; UF 102667, femur. MNI=2.

Description.—Among the leporid specimens from Leisey only the p3s are described and compared in detail, as other teeth and postcranial elements of both *Sylvilagus* and *Lepus* are generally considered to be nondiagnostic (White 1991a). Two p3s from Leisey 3A are similar in size to the p3 of *Sylvilagus floridanus*, *S. audubonii*, *S. transitionalis*, and *Lepus americanus*. The measurements of the Leisey *Sylvilagus* p3s are: UF 96220, length 3.1, width 3.0; UF 96221, length 3.0, width 2.5. The enamel pattern of these two teeth most closely resembles that of the p3 of *S. floridanus* in the presence of a single anterior reentrant, the lack of folding of the thick enamel on the anterior edge of the posteroexternal reentrant, and minimal folding of the thin enamel on the posterior edge of this reentrant (Fig. 1A). The Leisey p3s differ from *S. bachmani* and *S. nuttallii* by their larger size, from *S. aquaticus*, *S. palustris*, and *S. cunicularius* by smaller size, and from *S. brasiliensis* by the lack of multiple anterior reentrants. The recently described *S. webbi* (White 1991b) from the late Blancan and early Irvingtonian of Florida differs from the Leisey p3s in larger size, greater number of anterior reentrants, and more complex enamel folding. The Leisey specimens are referred to *S. floridanus* based on the similarity in size and enamel pattern of p3.

Remarks.—Leporids are notoriously difficult to identify from most cranial, dental, and postcranial remains. Paleontologists studying this family have tended to base their systematic conclusions on the structure of the p3, and to a lesser extent the P2 (e.g. White 1991a,b). The identification of *Sylvilagus floridanus* from the Leisey Shell Pit is based on two p3s from Leisey 3A. The referral of the additional teeth and postcranial elements from Leisey 1A and Leisey 3 to this species is based entirely on their small size, and therefore these identifications should be considered tentative.

The first *Sylvilagus* to appear in the Florida fossil record is *S. webbi* from the late Blancan Macasphalt Shell Pit and Kissimmee River local faunas. *S. webbi* also occurs in the earliest Irvingtonian Inglis 1A and De Soto Shell Pit local faunas and the late early Irvingtonian Haile 16A. Records of *S. floridanus* from Leisey and the correlative early Irvingtonian Payne Creek Mine and Haile 21A local faunas represent the earliest occurrence of this living species in Florida. The oldest records of *S. floridanus* are from the earliest Irvingtonian Curtis Ranch LF, Arizona and Vallecito Creek LF, California (White 1991a). Hibbard and Dalquest (1966) reported *Sylvilagus* cf. *S. floridanus* from the late early Irvingtonian Gilliland LF in Texas, a close correlative of Leisey based on the large mammal fauna (Morgan and Hulbert this volume).

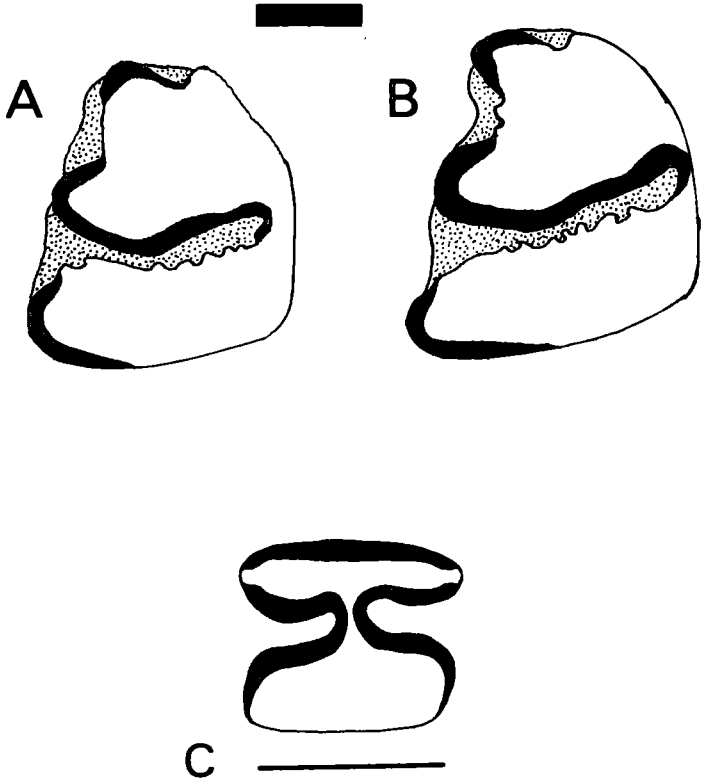


Figure 1. (A) *Sylvilagus floridanus*, Leisey 3A, right p3 (reversed), UF 96220; (B) *Lepus* cf. *L. townsendii*, Leisey 1A, left p3, UF 82165; (C) *Geomys pinetts*, Leisey 1A, left P4, UF 87225. Scale bar 1 mm in length for A and B and 2 mm in length for C.

Lepus cf. *L. townsendii* Bachman 1839

Referred Specimen.—Leisey 1A: UF 82165, left mandible with p3-p4. MNI=1.

Tentatively Referred Specimens.—Leisey 1A: UF 83659, distal humerus; UF 131992, partial innominate; UF 131993, distal femur.

Description.—The Leisey *Lepus* p3 can be distinguished from *Sylvilagus aquaticus*, *S. palustris*, and *S. cunicularius* by the single, slightly incised anterior reentrant and from all other species of *Sylvilagus* by its larger size (Fig. 1B). Measurements of the single p3 of *Lepus* (UF 82165) from Leisey are: length 3.5,

width 3.1. The Leisey tooth can be distinguished from *Lepus californicus*, *L. alleni*, *L. callotis*, and *L. flavigularis* by the slightly incised anterior reentrant, from *L. americanus* by the posteroexternal reentrant which extends to the lingual border of p3, and from *L. alleni*, *L. arcticus*, and *L. othus* by being smaller in size, falling below the observed ranges of the latter.

The Leisey p3 is tentatively referred to *Lepus townsendii* because it more closely resembles that species than other members of the genus. However, there are two features in which the Leisey tooth differs from extant *L. townsendii*. The anterior external reentrant on the Leisey p3 is slightly less well incised than in any of the 22 modern specimens of *L. townsendii* used for comparison. Also, Figure 1B shows that on UF 82165 from Leisey, the thin enamel on the posterior edge of the posteroexternal reentrant is moderately crenulated or folded. White (1991a) noted that this thin enamel was typically folded in *L. californicus* and unfolded in *L. townsendii*. The Leisey tooth differs from *L. californicus* and the extinct species *L. benjamini* from the early Irvingtonian Anita LF in Arizona (Hay 1921) by its shallower anterior reentrant and less complicated enamel. The Leisey *Lepus* is smaller than *L. giganteus* from the middle Irvingtonian Conard Fissure LF in Arkansas (Brown 1908).

The Leisey p3 differs from a large sample of *Lepus* p3s from the Inglis 1A LF in its smaller size, particularly the width. The Leisey and Inglis p3s are similar in having both the anterior reentrant and anteroexternal reentrant weakly incised. The thin enamel on the posterior edge of the posteroexternal reentrant ranges from simple and unfolded in some Inglis specimens to moderately crenulated in other Inglis specimens and the Leisey tooth. Further study of the Inglis sample may reveal that an undescribed species is present in Florida Irvingtonian faunas, but for now the Inglis jackrabbits are identified only as *Lepus* sp.. Both the Inglis 1A and Coleman 2A *Lepus* have been referred to *L. alleni* (see Martin 1974; Webb and Wilkins 1984). However, the p3s of the Inglis 1A *Lepus* can be distinguished from *L. alleni* by the weakly incised anterior reentrant and the lack of highly folded enamel. The *Lepus* sample from Coleman 2A consists entirely of postcranials (Martin 1974).

Remarks.—The identification of *Lepus* cf. *L. townsendii* from Leisey is based on a mandible with p3-p4. The three postcranial elements are tentatively referred to this species on the basis of their very large size compared to other leporid postcranials from Leisey. *Lepus* was first reported from Florida in the Coleman 2A and Inglis 1A Irvingtonian faunas (Martin 1974). Previously unreported specimens of *Lepus* from Florida include a femur from the middle Irvingtonian McLeod LF in Levy County and an edentulous mandibular symphysis (UF 128991) from the late early Irvingtonian Payne Creek Mine. The fossil record indicates that in Florida *Lepus* is restricted to the Irvingtonian.

The white-tailed jackrabbit *Lepus townsendii* is an extant species found on the Great Plains as far east as Illinois. Although Lundelius et al (1987) used the first

appearance of the genus *Lepus* as one of the defining taxa for the Irvingtonian NALMA, *Lepus* is now known from at least two very late Blancan faunas, Big Springs, Nebraska and Borchers, Kansas (White 1991a). White noted that both of these faunas contained some p3s that resembled *L. townsendii* and others that were more similar to *L. californicus*. This is very reminiscent of the sample of *Lepus* p3s from the Inglis 1A LF. Inglis is only slightly younger than Big Springs and Borchers, and represents the earliest record of *Lepus* in Florida.

Order RODENTIA Bowdich 1821
Family GEOMYIDAE Gill 1872
Geomys pinetis Rafinesque 1806

Referred Specimens.—Leisey 1A: UF 87225, partial right and left maxillae with left P4; UF 80044, 87964, right I1 (2); UF 88031, left I1; UF 125202, left mandible with i1, p4-m2; UF 83625, left mandible with p4; UF 81827, left i1; UF 83829, distal humerus. Leisey 3A: UF 125208, proximal ulna. Leisey 3: UF 124564, right mandible with i1, p4-m1. MNI=3.

Description.—Four specimens of *Geomys* from the Leisey Shell Pit LF, three from Leisey 1A and one from Leisey 3A, provide sufficient morphological information to permit an identification to the species level. A portion of the right and left maxillae with a P4 (UF 87225; Fig. 1C) is particularly significant, as the P4 is perhaps the single most diagnostic tooth used to document the evolutionary history of *Geomys* during the late Pliocene and Pleistocene of Florida (Wilkins 1984). The Leisey P4 is comparatively large (anteroposterior length 2.3, width of posterior loph 2.4) and totally lacks enamel on its posterior surface. Wilkins (1984) did not provide measurements of the upper dentition of Florida fossil *Geomys*, and thus no comparative measurements of the P4 are presented here. One or more P4s of *Geomys* are known from three other Irvingtonian sites in Florida: Inglis 1A, Haile 16A, and Coleman 2A. Wilkins (1984) stated that the *Geomys* from Inglis 1A and Haile 16A possessed enamel on at least half up to the entire posterior surface of P4, while specimens from Coleman 2A, as well as extant *G. pinetis*, lacked enamel in this region.

In an examination of the larger sample of *Geomys* now available from Haile 16A, a wider range of variation was noted in the amount of enamel on the posterior surface of P4 than was observed by Wilkins (1984). Because of its taxonomic importance, this character was re-examined for all Florida Blancan and Irvingtonian *Geomys*. Among 20 randomly selected P4s of the extinct species *G. propineta* (Wilkins 1984) from Inglis 1A (out of a total sample of over 100), 15 teeth (75%) have from 50-100% coverage of enamel on the posterior surface, 4 teeth (20%) have less than 50% coverage, and on 1 tooth the enamel is almost absent (coverage less than 5%, but still perceptible). The entire sample of 16 P4s

of *G. propineta* from Haile 16A was examined, of which only 4 teeth (25%) have 50-100% enamel coverage on the posterior surface, 7 teeth (44%) have less than 50% coverage, and in 5 teeth (31%) the enamel coverage is nearly to totally absent. Two P4s of *Geomys* (UF 100342, 104493) from the late Blancan Macaspalt Shell Pit LF in Sarasota County, Florida were examined as well. Both of these teeth are very similar to the majority of specimens of *G. propineta* from Inglis 1A in having nearly total coverage of enamel on their posterior surface. The single *Geomys* P4 from Leisey and a sample of six P4s from Coleman 2A resemble modern *G. pineta* in lacking enamel on their posterior surface.

The progressive loss of enamel on the posterior surface of P4 in Florida fossil *Geomys* from the late Pliocene and early Pleistocene provides a good indicator of age. *G. propineta* from the late Blancan Macaspalt Shell Pit LF and the earliest Irvingtonian Inglis 1A LF is characterized by having more than 50% of the posterior surface of P4 covered with enamel in most individuals, as well as by small size. Although the *Geomys* from Haile 16A is referred to *G. propineta* following Wilkins (1984), the enamel on the posterior edge of P4 in this sample is reduced compared to the two older samples. More than half of the P4s from Haile 16A have less than 50% enamel coverage on the posterior surface, including two teeth in which enamel is completely absent. It is not surprising that the Haile 16A *Geomys* is somewhat advanced over the sample from Inglis 1A, as other data suggest that the former site is younger. This character must have been evolving rapidly during the early Irvingtonian, because in the late early Irvingtonian Leisey Shell Pit LF, enamel was totally absent on the posterior surface of P4, a trait found in all younger samples referred to *G. pineta*. P4s of *G. pineta* from Leisey and Coleman 2A, as well as modern specimens of this species, are larger than those of *G. propineta* from Haile 16A, Inglis 1A, and Macaspalt.

Another important evolutionary trend in Florida *Geomys* is the increasing size and depth of the retromolar fossa through time (Wilkins 1984). The retromolar fossa is a pit located on the dorsal surface of the mandible posterolabial to the m2 and m3, and lingual to the coronoid process. The increase in size of the retromolar fossa is evident in the increasing distance between the base of the coronoid process and the toothrow labial to m2 and m3. The retromolar fossa is short, narrow, and very shallow in the Inglis 1A sample (Wilkins 1984). This fossa is noticeably longer and much deeper in modern *G. pineta*, and in fossil mandibles referred to this species from Leisey and Coleman. The anterior edge of the retromolar fossa is located posterolabial to the m2 and forms a nearly vertical plate in *G. pineta*, whereas the anterior margin slopes gradually posteriorly in mandibles of *G. propineta* from Inglis. Although no mandibles from Haile 16A preserving the retromolar fossa were available to Wilkins for study, one mandible is now known from this site (UF 69117) that preserves the anterior half of the retromolar fossa. The complete length and depth of the retromolar fossa cannot be determined from this specimen, but enough of this structure is preserved to confirm that it is very shallow and has a gently sloping anterior margin as in the Inglis

mandibles. The Leisey and Coleman mandibles are similar to modern *G. pinetis* in the size and depth of the retromolar fossa.

A third trend Wilkins (1984) observed in Florida *Geomys* was an increase in body size, using the observed range in width of the lower incisor as a size indicator. Although Wilkins (1984) noted that the width of i1 is dependent on the ontogenetic age of the individual, the maximum width of the i1 has increased through time. Only two lower incisors of *Geomys* are known from Leisey with widths of 1.7 and 2.2 mm (Table 2). Based on measurements in Wilkins (1984), this is slightly smaller than the maximum width of the i1 in modern *G. pinetis* (2.5 mm) and the range of lower incisor widths observed in the Coleman sample (1.9-2.5 mm). The maximum width of the Leisey lower incisors is broader than the i1s of *G. propineta* from Inglis 1A in which the maximum width is 1.9 mm (Wilkins 1984). Measurements of the two most complete mandibles of *Geomys* from Leisey are compared in Table 2 to mandibles from Haile 16A and Coleman 2A. Wilkins (1984) should be consulted for mandibular measurements of *G. propineta* from Inglis 1A and Recent *G. pinetis*. The measurements presented here and those of Wilkins (1984) indicate that the Leisey *Geomys* is intermediate in size between the smaller *G. propineta* from Inglis 1A and Haile 16A and the somewhat larger specimens of *G. pinetis* from Coleman 2A. The maximum size of modern *G. pinetis* apparently was achieved by the late Irvingtonian (Wilkins 1984).

Remarks.—Pocket gophers of the genus *Geomys* are first recorded in Florida from the late Blancan Macasphalt Shell Pit and Haile 15A local faunas (Morgan and Ridgway 1987). Based on small size and presence of enamel on the posterior surface of P4, the Macasphalt sample is referred to *G. propineta*, an extinct species originally described from the earliest Irvingtonian Inglis 1A LF (Wilkins 1984). The Haile 15A *Geomys* sample lacks a P4, but does possess a single specimen of the diagnostic M3 (Wilkins 1984) that closely resembles the M3 of *G. propineta*. A small sample of *Geomys* recently identified from the earliest Irvingtonian De Soto Shell Pit in De Soto County, a correlative of Inglis 1A, lacks the P4, M3, and mandibles, but is tentatively referred to *G. propineta* on the basis of small size and age. The *Geomys* sample from Haile 16A is referred to *G. propineta* following Wilkins (1984), but is somewhat more advanced than the Inglis pocket gopher in characters of the P4 and slightly larger size. The *Geomys* sample from the Leisey Shell Pit LF possesses characters of the extant species, *G. pinetis*, including the lack of enamel on the posterior surface of P4 and a large, deep retromolar fossa on the mandible, but is somewhat smaller. The living southeastern pocket gopher, *G. pinetis*, first appears in Florida at Leisey, presumably having evolved *in situ* from *G. propineta* during the early Irvingtonian. It is difficult to correlate the Florida Irvingtonian *Geomys* with other North American pocket gophers belonging to this

Table 2. Measurements (in mm) of lower incisors and cheek teeth of selected Irvingtonian *Geomys* from Florida. Description of measurements follows Wilkins (1984).

Locality	width i1	length p4	anterior width p4	posterior width p4	width m1
Haile 16A					
UF 69116	1.7	2.5	1.4	2.0	2.0
UF 69117	1.9	2.8	1.7	2.1	—
Leisey Shell Pit					
UF 125202	2.2	2.7	1.8	2.5	2.3
UF 125564	1.7	2.7	1.5	2.2	2.2
UF 83625	—	2.7	1.5	2.2	—
Coleman 2A					
UF 45861	2.5	2.8	1.7	2.4	2.6
UF 45864	2.2	2.9	1.6	2.3	2.4
UF 15001	—	2.9	1.9	2.5	—

genus because fossils of both *G. propineta* and *G. pineta* are restricted to Florida (Wilkins 1984). The extant species *G. pineta* has a rather limited distribution as well, occurring only in Florida, Georgia, and Alabama.

Family CASTORIDAE Gray 1821

Castoroides leiseyorum new species

Holotype.—UF 81736, posterior half of skull from Leisey Shell Pit 1A, Hillsborough County, Florida, Bermont Formation, late early Irvingtonian. Collected by Frank A. Garcia in August 1984.

Paratypes.—UF 60868, posterior half of skull from Leisey 1, collected by Frank A. Garcia in 1983; UF 115965, left mandible with i1, p4-m3 from Leisey 3, collected by Ralph Estevez and John Miller on 30 March 1988.

Referred Specimens.—**Leisey 1A:** UF 66000, incisor fragment; UF 83119, 86862, astragalus (2). **Leisey 3B:** UF 132047, partial cheektooth; **Leisey 3:** UF 124563, partial cheektooth. MNI=3.

Diagnosis.—*Castoroides leiseyorum* can be differentiated from *C. ohioensis*, the only other currently recognized species in the genus, by the absence of a mesopterygoid fossa on the basisphenoid. In *C. leiseyorum*, the basisphenoid bears a shallow elongated groove in the anatomical position where the deeply concave, ovate mesopterygoid fossa is located in *C. ohioensis*. *C. leiseyorum* can also be separated from *C. ohioensis* by characters of the lambdoidal crest. In *C. leiseyorum* this crest is lower and more rounded, and in dorsal view is strongly convex posterolaterally with a deep V-shaped indentation along the midline where it meets the sagittal crest. The lambdoidal crest is higher and sharper in *C. ohioensis*, and in dorsal view is more nearly parallel to the posterior margin of the skull. *C. leiseyorum* can be distinguished from *Procastoroides sweeti* by its larger size and the presence of well-developed longitudinal ridges and grooves on the incisors. *C. leiseyorum* differs from *P. idahoensis* in its larger size and by the presence of isolated enamel laminae on all lower cheek teeth resulting from the absence of enamel at the labial termination of the paraflexid and mesoflexid and the lingual termination of the hypoflexid.

Etymology.—Named for Bud Leisey and members of his family, as well as for the employees of the Leisey Shell Corporation. The study of paleontology in Florida has benefitted immeasurably from their cooperation and generosity.

Description.—The mandible and two braincases of *Castoroides* from Leisey are the most complete fossils of the giant beaver yet found in Florida. A nearly perfect left mandible (UF 115965) has a complete dentition, including an intact lower incisor. The mandibular ramus is virtually complete, with the exception of the coronoid process, the posterolateral portion of the capsular process, the posteriormost extremity of the angular process, and a portion of the ventral margin external to the incisor (Figs. 2A-C). The two partial skulls are nearly intact posterior to the interorbital constriction.

The mandible of *Castoroides leiseyorum* from Leisey was directly compared with specimens of *C. ohioensis* from various Florida Rancholabrean sites and with published descriptions, figures, and measurements of other complete mandibles of *C. ohioensis* from elsewhere in eastern North America. The Leisey mandible also was compared to literature descriptions and figures of the two Blancan taxa of giant beavers, *Procastoroides sweeti* (Barbour and Schultz 1937; Woodburne 1961) and *P. idahoensis* (Shotwell 1970). Like *C. ohioensis*, the lower incisor of the *C. leiseyorum* is strongly ridged or crenulated. The p4 of *C. leiseyorum* is very similar to that of typical *C. ohioensis* from the Rancholabrean. In both of these forms the paraflexid, mesoflexid, and hypoflexid extend entirely across the tooth from the labial to the lingual margin thereby completely isolating the four lophids as complete enamel laminae (dental terminology for castorid teeth follows Woodburne 1961). The mesoflexid and hypoflexid are also complete on the m1-

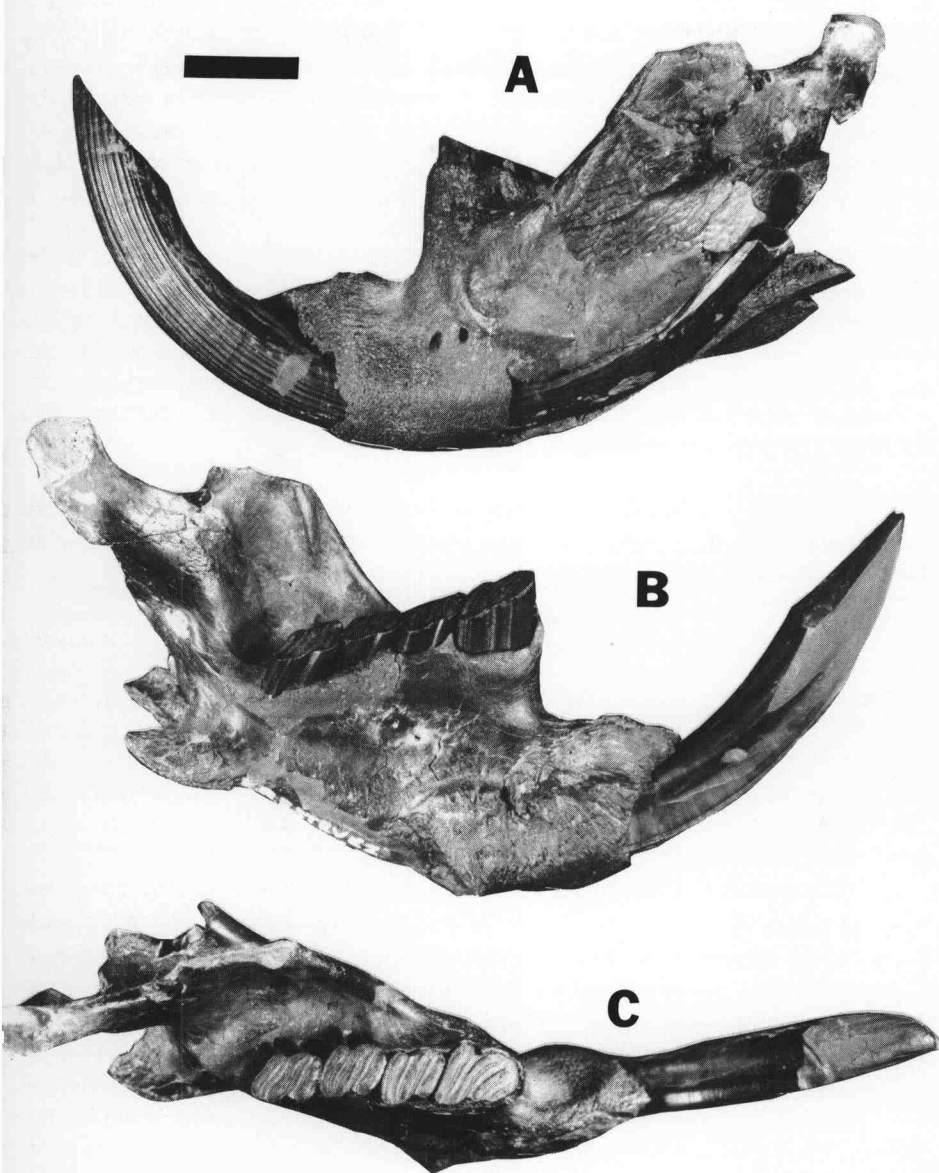


Figure 2. *Castoroides leiseyorum* new species, Leisey 3, left mandible with i1, p4-m3 (paratype), UF 115965. (A) lateral view; (B) medial view; (C) dorsal view. Scale bar 30 mm in length.

Table 3. Measurements (in mm) of the lower dentition of *Castoroides* and *Procastoroides*. Abbreviations are: L (length) and W (width). Mean, observed range, and sample size, respectively, are provided for all samples, except the single Leisey specimen.

Species	alveolar length p4-m3	occlusal length p4-m3	L i1	W i1	L p4
<i>Procastoroides sweeti</i>	—	50.3	11.5	10.4	12.3
Blancan		50-51	10.6-12.8	9.6-12.0	9.2-14.2
Kansas ¹		N=3	N=4	N=4	N=13
<i>Procastoroides idahoensis</i>	60.5	—	14.9	14.8	14.9
Blancan	—		—	—	14.6-15.1
Idaho ²	N=1		N=1	N=1	N=3
<i>Castoroides leiseyorum</i>					
Leisey Shell Pit					
UF 115965	73.2	69.6	23.3	20.8	22.1
<i>Castoroides ohioensis</i>	68	67	24.9	20.3	19.5
Florida	—	—	22.4-29.3	18.6-21.6	14.6-24.5
	N=1	N=1	N=7	N=7	N=6
<i>Castoroides ohioensis</i>	—	71.0	23.6	20.8	19.5
(exclusive of Florida) ³		70-72	20-27	20-22	19-20
		N=2	N=5	N=5	N=2

¹ Measurements from Woodburne (1961).

² Measurements from Shotwell (1970).

m3 and isolate the three lophids on each of these teeth. Furthermore, the enamel on the labial margin of the lophids is thin on all four cheekteeth of *C. leiseyorum*, especially on the labial edge of the median lophid. The lower cheekteeth of the Leisey mandible are similar in size to those of *C. ohioensis* from the Rancholabrean (Table 3). There appear to be no obvious differences between *C. leiseyorum* and *C. ohioensis* in the lower dentition and mandibular ramus.

Shotwell (1970) described the species *Procastoroides idahoensis* from the late Blancan Grand View LF in Idaho. Unlike the earlier Blancan species, *P. sweeti*, *P. idahoensis* has well developed longitudinal ridges on the incisors, like *Castoroides*. *P. idahoensis* is distinguished from *Castoroides* primarily by its smaller size, but also by the tendency for enamel to be present at the labial termination of the paraflexid and mesoflexid and lingual termination of the hypoflexid on the p4.

Table 3 Extended.

W p4	L m1	W m1	L m2	W m2	L m3	W m3
9.0 8.3-11.3 N=13	11.4 10.2-13.0 N=7	9.3 7.6-10.2 N=7	11.1 9.5-12.5 N=9	8.9 7.8-10.0 N=9	9.8 9.0-11.0 N=5	8.2 6.6-9.2 N=5
11.3 10.8-11.7 N=3	12.0 — N=1	13.1 — N=1	11.4 — N=1	10.9 — N=1	— —	— —
16.4	16.6	13.9	17.3	14.1	18.8	12.8
15.5 13.4-17.4 N=6	16.5 16.4-16.6 N=2	13.7 12.5-14.9 N=2	15.8 — N=1	14.6 — N=1	15.5 — N=1	12.9 — N=1
14.0 12-16 N=2	16.5 16-17 N=2	14.5 13-16 N=2	17.0 17 N=2	14.0 13-15 N=2	16 — N=1	12 — N=1

³ Measurements from Hay (1914) and Barbour (1931).

These terminations are composed of much thinner enamel than on the remainder of the tooth. In certain p4s of *P. idahoensis*, including the type, the paraflexid, mesoflexid, and hypoflexid extend entirely across the tooth as in *Castoroides*. The m1 from the type of *P. idahoensis* also has isolated enamel lophids like the p4; however, on the m2 of this specimen the medial and posterior lophids are connected by enamel at the lingual termination of the hypoflexid (Shotwell 1970). All of the lophids are isolated as complete enamel laminae on the four lower cheekteeth of the *C. leiseyorum* mandible.

Martin (1969) described an extinct subspecies of *Castoroides*, *C. ohioensis dilophidus*, from the Rancholabrean Santa Fe River 2 locality in northern peninsular Florida. This subspecies is characterized by the division of the 2nd anterior lophid on the p4 into two isolated elliptical enamel laminae. In *C. ohioensis* from elsewhere in North America both the 1st and 2nd anterior lophids

on p4 are undivided, consisting of single laminae. The single p4 of *C. leiseyorum* lacks the divided 2nd anterior lophid, and thus has the typical morphology of *C. ohioensis*.

The two braincases of *Castoroides leiseyorum* from Leisey (Figs. 3-4) provide much information on the posterior half of the skull. Stirton (1965) published excellent descriptions and figures of the skull of *C. ohioensis*. Detailed morphological comparisons were made between the two Leisey skulls and the figures and descriptions of *C. ohioensis* from Stirton. Cranial measurements are provided for the two skulls of *C. leiseyorum* (Table 4), and where possible, these are compared to measurements of five of the most complete skulls of late Pleistocene *C. ohioensis* (from Stirton 1965:276). Barbour and Schultz (1937, fig. 2) figured the holotype skull of *Procastoroides sweeti* from the Broadwater LF in Nebraska in dorsal and lateral views, and provided a very brief morphological description. They presented five cranial measurements for *P. sweeti*; however, most of these were based on a nearly complete skull (total length, zygomatic breadth, etc.), and thus cannot be compared to the incomplete Leisey skulls. Martin and Schultz (1985) figured and described a braincase of *P. idahoensis* from the late Blancan Seneca LF of Nebraska, but provided no measurements.

In most features of the braincase, *Castoroides leiseyorum* does not appear to differ significantly from *C. ohioensis*. Likewise, almost every one of the measurements taken on the two Leisey skulls (Table 4) is within the range of variation of the five *C. ohioensis* skulls measured by Stirton (1965). Many authors (e.g. Hay 1914; Stirton 1965) have noted that *Castoroides* is unique in possessing two separate posterior openings for the internal nares, one dorsal and one ventral. The posterodorsal opening, termed the mesopterygoid fossa by Stirton (1965), is perhaps the most unusual cranial feature of *Castoroides*, consisting of a large, deep fossa in the basisphenoid. The mesopterygoid fossa is ovate in outline, very deep, and opens anterodorsally into the internal narial passage. The ventral floor of this fossa is formed by expanded processes of the pterygoids. In a skull of *C. ohioensis* from McClean County, Illinois described by Stirton (1965), the mesopterygoid fossa is 23.0 mm in length and 15.8 mm in width. In another skull of *C. ohioensis* from Logansport, Indiana this opening is 25 mm long and 16 mm wide (Hay 1914).

Surprisingly, the dorsal mesopterygoid fossa, which is so characteristic of *Castoroides ohioensis*, is completely absent in the two braincases of *C. leiseyorum*, both of which have reasonably complete basicranial regions (Figs. 3B, 4B). In the two Leisey skulls, the basisphenoid is well preserved and it lacks the large, deep, ovate fossa for the posterodorsal opening of the internal narial passage. Instead, the basisphenoid in *C. leiseyorum* bears a slightly concave, elongated groove along the midline. This groove connects anteriorly to the internal narial opening in the paratype skull (UF 60868), although that portion of the basicranial region anterior to the basisphenoid is absent in the holotype (UF 81736). Both Leisey skulls are

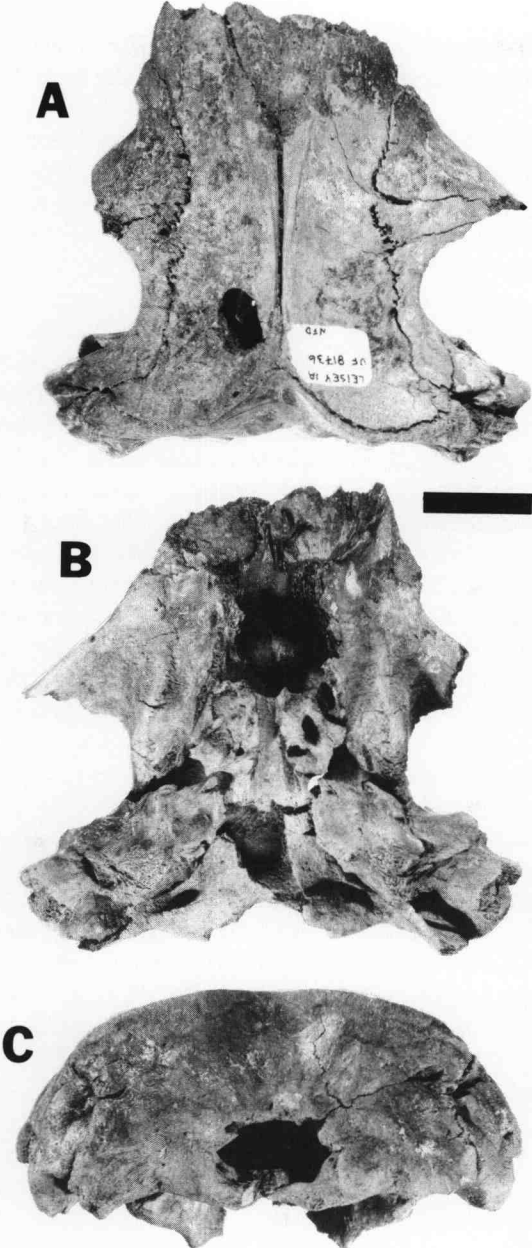


Figure 3. *Castoroides leiseyorum* new species, Leisey 1A, braincase (holotype), UF 81736. (A) dorsal view; (B) ventral view; (C) posterior view. Scale bar 30 mm in length.

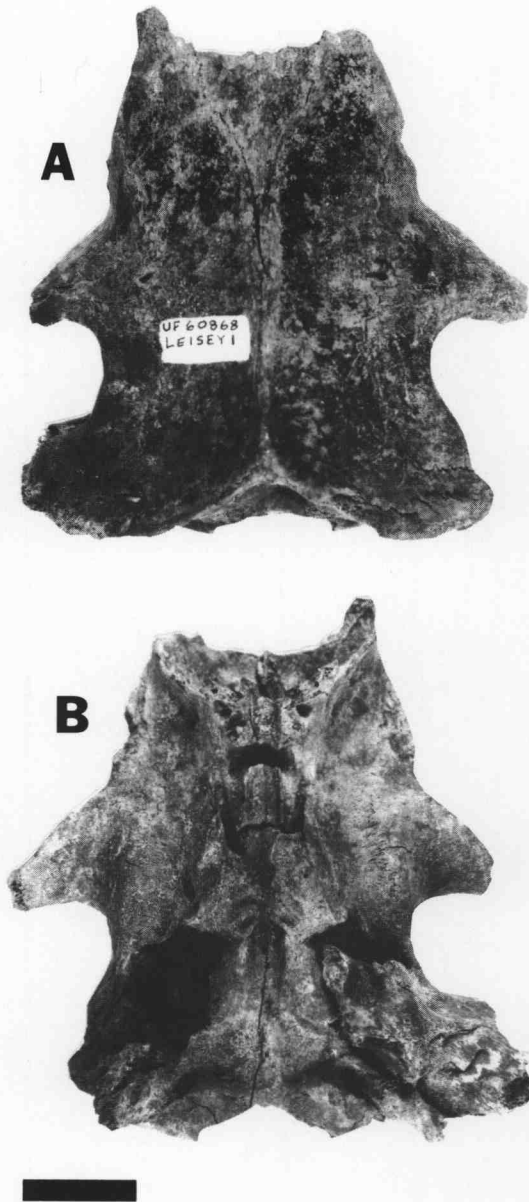


Figure 4. *Castoroides leiseyorum* new species, Leisey 1, braincase (paratype), UF 60868. (A) dorsal view; (B) ventral view. Scale bar 30 mm in length.

Table 4. Selected cranial measurements (in mm) of *Castoroides leiseyorum* from the Leisey Shell Pit LF and late Pleistocene *Castoroides ohioensis*. Means and observed ranges, respectively, for the *C. ohioensis* sample were computed from measurements of five of the most complete skulls of this species from Rancholabrean sites in the northern United States provided by Stirton (1965, p. 276).

Species	width of postzygomatic constriction	width of mastoid processes	width of paroccipital processes	depth of braincase	breadth of occipital condyles	breadth of foramen magnum	height of foramen magnum
<i>Castoroides leiseyorum</i>							
Leisey Shell Pit							
UF 60868	79.8	—	—	62.8	57.0	31.6	18.7
UF 81736	77.8	141.4	109.6	60.6	62.3	33.4	19.3
<i>Castoroides ohioensis</i>							
Rancholabrean	81.2	152.4	111.6	64.9	66.5	30.4	15.4
	71.5-88.2	136.5-167.0	101.0-123.0	62.2-68.0	—	—	—
	N=5	N=5	N=5	N=5	N=1	N=1	N=1

damaged in the pterygoid region, but appear to have possessed expanded pterygoid processes that would have formed a ventral floor beneath the anterior portion of the basisphenoid, as in *C. ohioensis*.

Based on the presence of an incipiently concave basisphenoid that connects anteriorly to the internal narial opening and a ventral floor formed by the pterygoids, it appears that the two early Pleistocene *Castoroides* skulls from Leisey possessed the early morphological stages of the deep mesopterygoid fossa and double internal nares characteristic of the late Pleistocene *C. ohioensis*. The timing of the earliest appearance of a fully developed mesopterygoid fossa in *Castoroides* must await the discovery of skulls from middle and late Irvingtonian sites. The basicranial region in the two species of *Procastoroides* has not been described, although braincases are known for both *P. sweeti* and *P. idahoensis* (Barbour and Schultz 1937; Martin and Schultz 1985).

The basioccipital of the two *Castoroides leiseyorum* skulls also appears to be somewhat different from Rancholabrean specimens of *C. ohioensis*. There is a slight ridge along the midline of the basioccipital in the Leisey skulls and the portion of the basioccipital lateral to this ridge is only slightly concave. In *C. ohioensis*, the median ridge is higher and sharper and laterally the basioccipital is more concave. Both species of *Castoroides* are very different from the modern beaver *Castor* in the basicranial region. *Castor* lacks a concavity in the basisphenoid and has only a single internal narial opening. However, *Castor* has a very prominent, deep, rectangular fossa that occupies virtually the entire basioccipital. There is no evidence of a concavity in the basioccipital in either species of *Castoroides*.

The lambdoidal crests in the two braincases of *Castoroides leiseyorum* differ in shape from typical *C. ohioensis*. In the two Leisey *Castoroides* skulls the lambdoidal crest is lower and more rounded. In dorsal aspect this crest is strongly convex or rounded posterolaterally and then curves sharply anteriorly for a distance of 15-20 mm at the midline forming a very distinct V-shaped outline (see Figs. 3A, 4A). The lambdoidal crest of *C. ohioensis* is sharper and more vertical, and in dorsal view is more parallel to the posterior margin of the skull meeting the sagittal crest at nearly a right angle.

Remarks.—The Leisey Shell Pit LF has produced the best preserved fossils of *Castoroides* known from Florida. Isolated teeth, especially fragments of the characteristic ridged incisors, as well as limb bones are relatively common in certain Florida Rancholabrean sites, but more intact material is extremely scarce. A few partial mandibles with cheekteeth and several unbroken incisors were the most complete specimens of the giant beaver known from Florida prior to the discovery of Leisey.

The Leisey Shell Pit LF represents the oldest well-documented occurrence of *Castoroides* in Florida. The only other securely dated Irvingtonian record of *Castoroides* from Florida consists of a complete upper incisor (UF 17318), two

isolated cheekteeth (UF 17319-17320), and an atlas (UF 133904) from the Crystal River Power Plant LF in Citrus County, an early Irvingtonian correlative of Leisey. A fragmentary braincase of *Castoroides* (UF 60860) from Apollo Beach, located about 10 km north of Leisey, is probably Irvingtonian as well, although the Apollo Beach fauna is a mixed assemblage containing both Irvingtonian and Rancholabrean taxa. The Apollo Beach *Castoroides* skull lacks the critical basicranial region, and thus can not be definitely referred to *C. leiseyorum*.

Martin (1969) reported three isolated teeth and an incisor fragment of *Castoroides* sp. from the supposed late Blancan Santa Fe 1B Site in Columbia County in northern peninsular Florida. However, examination of the mammalian fauna from Santa Fe 1B reveals that this site, like many of the Santa Fe faunas, consists of a mixture of late Blancan and Rancholabrean taxa (Morgan and Ridgway 1987; Morgan and Hulbert this volume). Based on the absence of *Castoroides* from all other late Blancan and earliest Irvingtonian faunas in Florida, it appears highly probable that the Santa Fe 1B teeth are Rancholabrean in age. Removing this single questionable Blancan record, *C. leiseyorum* from the Leisey Shell Pit appears to be the oldest well documented sample of *Castoroides*. *C. leiseyorum* probably was derived from a species of *Procastoroides* sometime during the late Blancan or earliest Irvingtonian.

Martin (1969) summarized the systematics and distribution of *Castoroides ohioensis* in Florida. He listed 25 Rancholabrean faunas from Florida containing *C. ohioensis*, most of which sampled freshwater depositional environments. Martin described the subspecies *C. ohioensis dilophidus* from several late Pleistocene localities in the Santa Fe River system. Martin (1975) later reported specimens of *C. ohioensis dilophidus* from Rancholabrean deposits in the Waccasassa River in Levy County, Florida. The UF Collection now has additional material of *C. ohioensis dilophidus* from the Oklawaha River and Withlacoochee River in Marion County and from a site near the Suwannee River at Branford in Suwannee County. Although Martin (1969, 1975) suggested that *C. ohioensis dilophidus* was restricted to the Santa Fe River and its drainages during the late Pleistocene, these new records indicate that *C. ohioensis dilophidus* was more widespread in northern peninsular Florida during the late Pleistocene.

Family ERETHIZONTIDAE Thomas 1897

Erethizon dorsatum (Linnaeus 1758)

Referred Specimens.--Leisey 3: UF 124632, left mandible with p4-m2; UF 128200, left mandible with p4-m3 (cast); UF 135669, left mandible with i1, m1-m2. MNI=3.

Description.—The three Leisey porcupine mandibles (Figs. 5A-C) are similar to *Erethizon* and differ from *Coendou* in the characters discussed by White (1968, 1970) and Frazier (1981). Among other characters, these two genera can be separated by the degree of anterior to posterior divergence of the lower toothrows from the midline. The lower toothrows of *Coendou* are parallel or subparallel, diverging from the midline only slightly posteriorly, whereas the toothrows of *Erethizon* diverge noticeably. In an isolated mandible the degree of divergence can be estimated by drawing an imaginary line through the longitudinal axis of the toothrow. In *Coendou* this line generally falls lateral to the lower incisor and in *Erethizon* it falls medial to the incisor. In the three Leisey mandibles the toothrows diverge strongly from the midline from anterior to posterior, and a line projected through the toothrows falls medial to the incisor, both of which suggest referral to *Erethizon*.

With the exception of the small species *Erethizon kleini* from Inglis 1A, the Leisey mandibles and all other Florida erethizontid fossils are larger than living species of the Neotropical porcupine *Coendou* (see comparative measurements of *Erethizon* and *Coendou* in Frazier 1981). There is no overlap in size between these two genera in the alveolar length of the lower toothrow. The largest mandible of *Coendou* from a sample of 114 measured by Frazier (1981) had an alveolar toothrow length of 23.7 mm (sample mean = 19.4), while the smallest *Erethizon* from a sample of 154 was 25.3 mm (sample mean = 29.1). The two Leisey mandibles in which this measurement can be taken both have alveolar toothrows in excess of 31 mm (Table 5), placing them well above the size range of *Coendou* and near the maximum size for the living porcupine, *Erethizon dorsatum*.

Frazier (1981) distinguished *Erethizon kleini* from *E. dorsatum* primarily on the basis of its smaller size. The three porcupine mandibles from the Leisey Shell Pit LF are considerably larger than *E. kleini* (see measurements in Table 5). The Leisey mandibles are within the range of variation of *E. dorsatum* in all available measurements, but are generally larger than the average modern *E. dorsatum*. The Inglis *Erethizon* jaws and lower teeth are either smaller than *E. dorsatum* or are at the low end of the range of variation of the modern species. Other Irvingtonian specimens from Florida referred to *E. dorsatum* also tend to be large (Table 5). On the basis of both size and morphology the porcupine mandibles from Leisey are indistinguishable from extant *E. dorsatum*.

Remarks.—Frazier (1981) reviewed the fossil history of North American porcupines. He described a new small species of *Erethizon*, *E. kleini*, from the earliest Irvingtonian Inglis 1A LF, along with two referred maxillae from Merritt Island in Brevard County. Frazier reported *E. dorsatum* from several Florida Irvingtonian sites, including Haile 16A, Apollo Beach, and Coleman 2A. The *Erethizon* mandibles from Leisey and Haile 16A are very similar in size and morphology, reflecting the overall similarity between the rodent faunas in these two sites (Table 5). Although smaller in some measurements, the sample of three

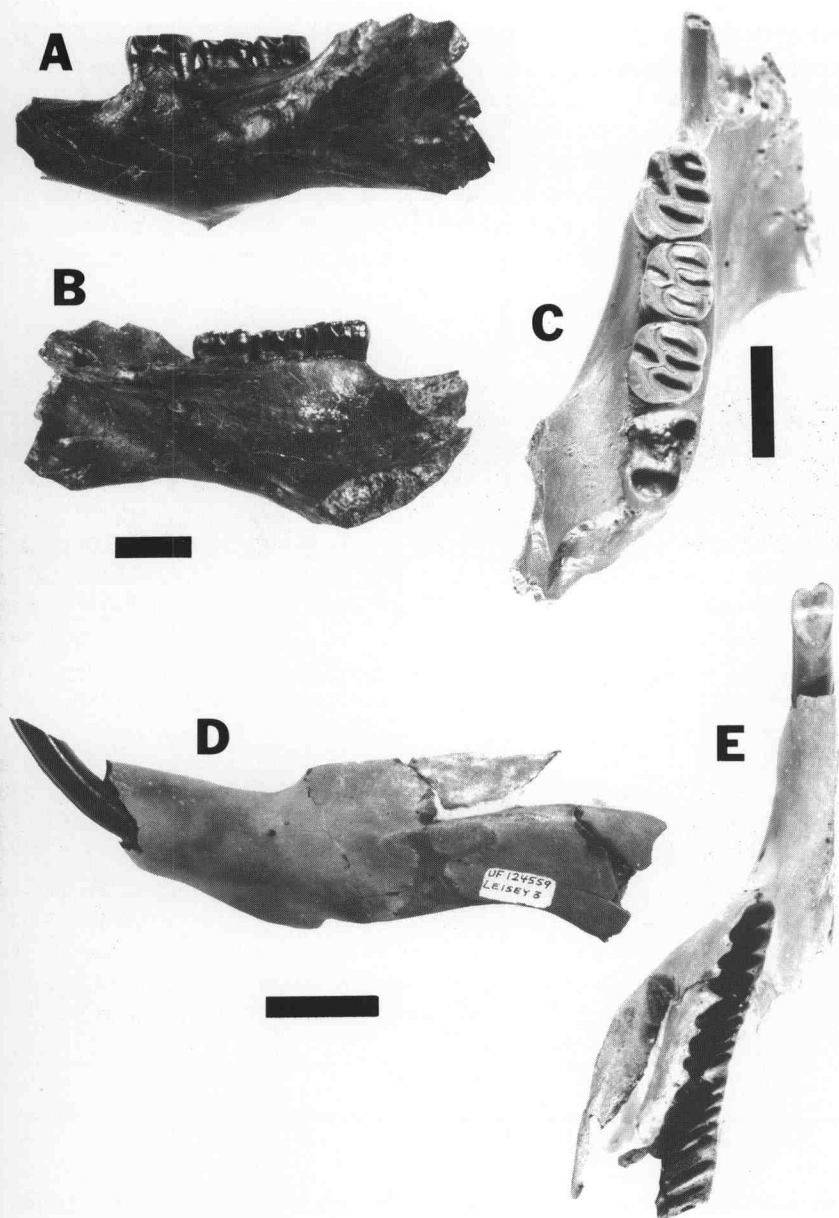


Figure 5. *Erethizon dorsatum*, Leisey 3, left mandible with p4-m2, UF 124632. (A) lateral view; (B) medial view; (C) dorsal view. *Nechoerus* sp., Leisey 3, left mandible with i1, UF 124559. (D) lateral view; (E) dorsal view. Scale bars for A and B (under B) and C (right of C) both 10 mm in length. Scale bar for D and E (under D) 30 mm in length.

Table 5. Mandibular measurements (in mm) of late Pliocene and Pleistocene *Erethizon* from Florida.

Species	alveolar length of lower toothrow	depth of mandible at p4	depth of mandible at m2	length of diastema	length of symphysis	length p4	width p4
<i>Erethizon</i> sp.							
Haile 7C							
UF 121740	32.6	-	-	-	-	8.0	6.6
<i>Erethizon kleini</i>							
Inglis 1A							
UF 21473 (type)	25.7	22.9	14.4	16.3	30.9	7.1	5.9
UF 21474	24.7	20.4	14.2	12.9	28.0	6.7	5.6
UF 21475	-	-	15.1	-	-	-	-
<i>Erethizon dorsatum</i>							
Haile 16A							
UF 21490	30.6	28.9	20.1	24.5	41.4	8.4	7.1
UF 21492	-	-	-	-	-	-	-
<i>Erethizon dorsatum</i>							
Leisey 3							
UF 124632	31.3	26.1	17.0	-	-	8.9	7.2
UF 128200	31.6	26.4	16.9	20.1	36.4	8.8	7.2
UF 135669	-	27.4	17.2	-	-	-	-
<i>Erethizon dorsatum</i>							
Apollo Beach							
UF 24112	-	21.8	15.2	-	-	-	-
UF 24113	-	-	-	-	-	7.7	6.8
UF 24114	28.6	21.8	16.7	-	-	8.1	6.6
<i>Erethizon dorsatum</i>							
Aucilla River							
UF 92392	28.2	22.5	13.8	15.8	31.6	7.5	6.1
<i>Erethizon dorsatum</i> ¹							
Recent (n=154)							
mean	29.1	25.1	16.0	22.8	36.5	-	7.5
range	25.3-	20.1-	12.2-	17.3-	29.6-	-	6.0-
	33.1	30.2	18.9	27.9	44.4	-	9.0

Erethizon mandibles from Apollo Beach is generally similar to the three Leisey specimens as well, further indicating an Irvingtonian age for at least a portion of the Apollo Beach fauna. The late early Irvingtonian Haile 16A and Leisey Shell Pit local faunas, and perhaps the Apollo Beach LF as well, appear to represent the oldest records of *E. dorsatum*. The earliest previous records of *E. dorsatum* were

Table 5 Extended.

Species	length m1	width m1	length m2	width m2	length m3	width m3
<i>Erethizon</i> sp.						
Haile 7C						
UF 121740	7.5	6.5	7.4	7.1	6.7	6.0
<i>Erethizon kleini</i>						
Inglis 1A						
UF 21473 (type)	6.0	5.5	6.0	5.9	5.9	5.4
UF 21474	5.5	5.3	6.0	5.8	—	—
UF 21475	5.9	5.4	6.0	5.9	5.5	5.1
<i>Erethizon dorsatum</i>						
Haile 16A						
UF 21490	7.0	6.7	7.1	7.0	7.5	6.7
UF 21492	7.1	6.4	7.3	6.9	—	—
<i>Erethizon dorsatum</i>						
Leisey 3						
UF 124632	7.0	6.5	7.2	6.6	—	—
UF 128200	7.4	6.7	7.2	7.0	7.1	6.4
UF 135669	7.0	6.5	6.9	6.5	—	—
<i>Erethizon dorsatum</i>						
Apollo Beach						
UF 24112	7.3	6.9	7.1	7.1	—	—
UF 24113	6.4	6.2	6.7	6.7	—	—
UF 24114	6.5	6.1	6.3	6.1	6.1	5.5
<i>Erethizon dorsatum</i>						
Aucilla River						
UF 92392	5.6	5.2	5.9	6.1	6.2	5.7
<i>Erethizon dorsatum</i> ¹						
Recent (n=154)						
mean	—	6.4	—	—	—	—
range	—	5.3-	—	—	—	—
	—	7.9	—	—	—	—

¹ Measurements from Frazier (1981, Table 1).

from middle Irvingtonian faunas, including Cumberland Cave, Port Kennedy Cave, Trout Cave, and Conard Fissure (Frazier 1981).

Since the publication of Frazier's (1981) review, fossils of *Erethizon* have been recovered from three additional Florida sites, including the Leisey Shell Pit. The other new sites represent the oldest and youngest well-documented records of porcupines in Florida. An associated palate and mandible from the latest Blancan

Haile 7C LF (UF 121740) is the only Florida Blancan occurrence of *Erethizon*, and the earliest record of the genus in eastern North America (Hulbert et al. 1989). This specimen is much larger than *E. kleini* and somewhat larger than *E. dorsatum* (Table 5). It is comparable in size to *E. bathygnathum* from the late Blancan and early Irvingtonian of the western United States. The youngest porcupine fossil from Florida is a complete mandible with full dentition (UF 92392) of *E. dorsatum* from the late Rancholabrean Aucilla River LF in Taylor County in the eastern panhandle. The closest records of extant *E. dorsatum* are from southern Tennessee to the north and central Texas to the west (Hall 1981).

Family HYDROCHAERIDAE Gill 1872

Nechoerus sp.

Referred Specimens.—Leisey 1A: UF 83244, 83828, 86942, I1 (3); UF 66101, 95881, i1 (2); UF 66102, 86149, partial m2 (2); UF 66104, proximal radius; UF 65400, proximal ulna; UF 66103, 88374, 115736, proximal femur (3); UF 87967, astragalus. Leisey 3: UF 124173, right mandible (edentulous); UF 124559, left mandible with i1; UF 124560, symphysis of left mandible; UF 124561, partial m1; UF 124562, m2. MNI=4.

Description.—The capybara sample from Leisey primarily consists of fragmentary teeth and partial postcranial elements that are not diagnostic below the family level. However, two mandibles (UF 124559, UF 124173) from Leisey 3 are complete enough to permit an identification to genus. Ahearn and Lance (1980) and Ahearn (1981) described several important characters of the mandible and dentition that reliably separate the extant genus of capybara, *Hydrochaeris*, from the extinct giant capybara, *Nechoerus*. The spelling of *Hydrochaeris* used here follows the recommendation of Husson (1978), although the spelling *Hydrochoerus* is more common in the literature (e.g. Kurtén and Anderson 1980; Mones and Ojasti 1986). We follow the dental terminology for capybara teeth used by Ahearn and Lance (1980).

The location of the masseteric fossa and extent of the masseteric ridge, which forms a bony shelf on the lateral surface of the dentary for the insertion of the masseter muscle, differ between the two genera. In *Nechoerus*, the anterior extremity of the masseteric ridge terminates lateral to the third prism of the p4 and the anterior portion of the masseteric fossa is opposite the posterior edge of p4. The masseteric ridge extends farther anteriorly in *Hydrochaeris* to the level of the first or second prism of p4, and the anteriormost extension of the masseteric fossa is more anterior as well. Another character separating these two genera is the external structure of the incisor enamel. *Hydrochaeris* has a weak groove on the lower and upper incisors, but lacks distinctly ridged enamel. *Nechoerus* has a

deep groove and strongly ridged enamel on both incisors. *Nechoerus* is also generally larger than *Hydrochaeris*.

In characters of the masseteric ridge and fossa, as well as size, the two hydrochaerid mandibles from Leisey are clearly referable to *Nechoerus*. In both of these specimens, the masseteric ridge terminates opposite the alveolus for the third prism of p4 and the masseteric fossa extends to the level of, or very slightly anterior to, the posterior edge of p4 (see Figs. 5D-E). The two Leisey mandibles are considerably larger than modern comparative specimens of adult *Hydrochaeris* in the UF Mammalogy Collection, but are smaller than several RanchoLabrean mandibles of *N. pinckneyi* examined from Florida, including UF 9763 from the Ichetucknee River in Columbia County and UF 23497 from Octopus Cave in Levy County. All hydrochaerid incisor fragments from Leisey have a well developed groove and at least some evidence of the longitudinal ridges characteristic of *Nechoerus*, although in most specimens the ridges are not as well developed as in the larger *N. pinckneyi*. One upper incisor fragment from Leisey (UF 83828) has strongly ridged enamel.

Although the Leisey mandibles are confidently referred to *Nechoerus*, they lack the diagnostic features to permit an identification to the species level. Two species of *Nechoerus* have been identified from Florida, *N. dichroplax* from several late Blancan faunas and *N. pinckneyi* from numerous late RanchoLabrean faunas (Ahearn and Lance 1980; Kurtén and Anderson 1980; Ahearn 1981). These two species are distinguished from one another and from other species of *Nechoerus*, most of which are restricted to South America, by characters of the dentition, primarily the M3 and p4. As noted above, the two most complete Leisey *Nechoerus* mandibles lack cheekteeth. Several isolated cheekteeth are present in the Leisey sample, but these are all fragmentary, and do not include the diagnostic M3 or p4.

Nechoerus dichroplax is characterized by having split or bifurcated laminae on the labial edge of M3. This species also can be separated from *N. pinckneyi* by its relatively shorter p4 in which the connection between the first and second prisms is reduced and the second labial fissure is directed between the second and third prisms. Two capybara mandibles from the late Blancan Macasphalt Shell Pit LF have complete p4s and the anterior portion of the masseteric ridge preserved, a juvenile left mandible with p4-m1 (UF 60858) and an adult right mandible with p4 (UF 94630). In both mandibles the masseteric ridge extends anteriorly opposite the third prism of the p4, and in the adult specimen the incisor enamel is strongly ridged as is typical of *Nechoerus*. The p4 in both specimens has the morphology of *N. dichroplax* in which the connection between the first and second prisms is reduced and the second labial fissure is directed between the second and third prisms (Ahearn and Lance 1980).

Based on the two Leisey mandibles, as well as several partial M3s from the apparently correlative Apollo Beach fauna, there may be a third species of *Nechoerus* from Florida that occurred during the early Irvingtonian. This

capybara cannot be confidently separated from *N. dichroplax* based on the available mandibles, but the M3s from Apollo Beach lack the characteristic bifurcations of the Blancan species. The two edentulous mandibles of *Neochoerus* from Leisey resemble the adult mandible of *N. dichroplax* from the Macasphalt Shell Pit. However, the diagnostic occlusal pattern of the p4 cannot be accurately determined from the empty alveoli in the Leisey mandibles. Mandibles of *N. pinckneyi* are larger than those of *Neochoerus* from Leisey and *N. dichroplax* from Macasphalt, and the p4 is considerably more elongated, a feature that can be ascertained from the alveolus. Only more complete material of Irvingtonian *Neochoerus* from Florida will permit a definite allocation to species. The fragmentary *Neochoerus* teeth from Apollo Beach were referred to *N. pinckneyi* by Ahearn (1981), but are here placed in *Neochoerus* sp. along with the Leisey sample. The Leisey material is either referable to *N. dichroplax* or it represents a new species, it is not conspecific with Rancholabrean *N. pinckneyi*.

Remarks.—Ahearn (1981) reviewed the fossil record of the Hydrochaeridae in North America. She recognized three species of capybaras from late Pliocene and Pleistocene sites in Florida: *Neochoerus dichroplax* from the late Blancan, *N. pinckneyi* from the Irvingtonian and Rancholabrean, and *Hydrochaeris holmesi* from the late Blancan through the Rancholabrean. Although hydrochaerids are fairly common in Florida Blancan, Irvingtonian, and Rancholabrean faunas, they are rare in other North American Plio-Pleistocene sites. Ahearn and Lance (1980) described *N. dichroplax* from the late Blancan Dry Mountain and 111 Ranch faunas in Arizona, with referred specimens from two late Blancan localities in southwestern Florida, Sommer's Pit in Sarasota County and Mule Pen Quarry in Collier County. Morgan and Ridgway (1987) have since reported *N. dichroplax* from the late Blancan Macasphalt Shell Pit in Sarasota County. Morgan and Hulbert (this volume) list hydrochaerids from several additional Florida late Blancan local faunas, but this material is too fragmentary for a generic allocation. *Neochoerus* was one of the first Neotropical immigrants to reach North America in the late Pliocene (late Blancan) during the Great American Interchange. The late Blancan *Neochoerus* from Arizona and Florida represent the earliest North American records of capybaras (Ahearn and Lance 1980). The association of *Neochoerus* with certain indigenous North American taxa, in particular *Nannippus peninsulatus*, is characteristic of the late Blancan between about 2.5 and 2.0 Ma.

Pending discovery of more diagnostic material, the early Irvingtonian *Neochoerus* from Florida cannot be identified to species. This capybara is either conspecific with *N. dichroplax*, thereby extending the chronologic range of that species into the early Irvingtonian, or it represents an undescribed form. Ahearn (1981) gave the chronologic range of *N. pinckneyi* in Florida as middle or late Irvingtonian through late Rancholabrean. She listed only two Irvingtonian sites for this species, Santa Fe 2A and Apollo Beach. Further study indicates that the Santa Fe 2A fauna is Rancholabrean, whereas the Apollo Beach *Neochoerus* is

probably not referable to *N. pinckneyi*. The Apollo Beach fauna is a mixed assemblage consisting of both Irvingtonian and Rancholabrean species. Many mammals in the Apollo Beach fauna, including *Castoroides* sp., *Erethizon dorsatum*, *Arctodus pristinus*, and *Tapirus haysii*, are similar to those from the nearby Leisey Shell Pit and are probably early Irvingtonian in age. *N. pinckneyi* is restricted to the Rancholabrean in Florida where it is fairly common, particularly in sites that sample freshwater depositional environments such as streams, springs, and lakes. *Castoroides ohioensis* and *Tapirus veroensis* are common faunal associates of *N. pinckneyi* in Florida late Rancholabrean riverine faunas.

A third and somewhat smaller species of extinct capybara, *Hydrochaeris holmesi*, was described by Simpson (1928) from the late Rancholabrean Sabertooth Cave LF in Citrus County, Florida. Subsequently *H. holmesi* has been reported from numerous other Florida sites ranging in age from late Blancan to late Rancholabrean (Kurtén and Anderson 1980; Ahearn 1981). Pre-Rancholabrean records of *H. holmesi* include the late Blancan Haile 15A LF, the earliest Irvingtonian Inglis 1A LF, and the late Irvingtonian Coleman 2A LF (Ahearn 1981).

There is some confusion regarding the generic identification of North American fossil capybaras. Although most previous authors (e.g. Kurtén and Anderson 1980; Ahearn 1981) recognized two genera of fossil capybaras from Florida, *Hydrochaeris* and *Neochoerus*, Mones and Ojasti (1986:1) stated that, "References to fossil *Hydrochoerus* in North America...are misidentifications of *Neochoerus* (Mones 1984)." *Hydrochaeris holmesi* was regarded as a synonym of *Neochoerus aesopi* (= *N. pinckneyi*) by Mones (1984), although he did not provide morphological descriptions or further justification for this taxonomic decision. Until more thorough morphological comparisons are conducted, it seems most prudent to continue recognition of *H. holmesi*.

Family MURIDAE Gray 1821
Subfamily SIGMODONTINAE Thomas 1897
Sigmodon libitinus Martin 1979

Referred Specimens.--Leisey 1A: UF 132070, partial right M2; UF 132071, left M3. Leisey 3A: UF 124588, right maxilla with M1-M2; UF 124331, left maxilla with M1; UF 124329, 124586, right mandible with m1-m2 (2); UF 124587, left mandible with m1-m2; UF 124325, right mandible with m2; UF 124314, right mandible with m3; UF 124310, 124313, 124319, 124320, 125210, 128965, 128966, 132057, right M1 (8); UF 124312, 124326, 124589, 128967, left M1 (4); UF 124590, 125209, 128968, left M2 (3); UF 124315, 124322, 132058, right M3 (3); UF 124321, 128971, 132059, right m1 (3); UF 128972-128975, 132060, left m1 (5); UF 124311, 124316, 124317, 128976, right m2 (4); UF

124318, right m3; UF 124323, 124324, 124327, 128977, 132061, left m3 (5).
Leisey 3B: UF 132054, edentulous left maxilla; UF 132055, right m3. MNI=11.

Description.—A species of the genus *Sigmodon* is the most abundant rodent at Leisey where it is represented by more than 50 specimens of maxillae, mandibles, and isolated teeth from a minimum of 11 individuals. Six species of *Sigmodon* are now known from late Pliocene and Pleistocene sites in Florida. Four of these species of cotton rats, *S. curtisi*, *S. minor*, *S. libitinus*, and *S. bakeri*, are found in Irvingtonian faunas, while *S. medius* occurs only in late Blancan faunas and *S. hispidus* is restricted to the Rancholabrean and Recent. The Leisey *Sigmodon* were directly compared to Florida samples of all six of these species, including: five mandibles of *S. medius* from the late Blancan Macasphalt Shell Pit LF, 20 mandibles of *S. curtisi* from the earliest Irvingtonian Inglis 1A LF, two isolated teeth of *S. minor* from the earliest Irvingtonian De Soto Shell Pit LF in De Soto County, 20 mandibles of *S. libitinus* from the early Irvingtonian Haile 16A, 12 mandibles of *S. bakeri* from the late Irvingtonian Coleman 2A LF, and a large sample of modern *S. hispidus* from northern peninsular Florida.

Martin (1979) provided descriptions, diagnoses, and measurements for the various extinct and living species of *Sigmodon*. Following Martin, most comparisons and measurements of the species of *Sigmodon* are based on the lower dentition. The most important morphological changes in *Sigmodon* occur on the m1, with some characters on the m2 and m3 as well. The presence or absence of small accessory roots on m1 is an important character in the evolutionary history of *Sigmodon*. The most primitive species, *S. medius*, generally possesses only the primary anterior and posterior roots, and small accessory roots are lacking. Most Irvingtonian species of *Sigmodon*, including *S. curtisi* and *S. libitinus*, have three roots, including a small accessory labial root in addition to the two primary roots. The more advanced species in the genus, including *S. bakeri* and *S. hispidus*, have four roots on m1, the two primary roots and both a labial and a lingual accessory root. Another important dental feature of the m1 is the structure of the anteroconid. The two Pliocene species, *S. medius* and *S. curtisi*, as well as *S. hispidus*, tend to have symmetrical anteroconids on m1, whereas *S. libitinus* and *S. bakeri* both have asymmetrical anteroconids resulting from a moderately to well developed posterolabial extension.

The presence or absence of an anterior cingulid on m2 and m3 helps to differentiate several species of *Sigmodon*. *S. medius*, *S. curtisi*, and *S. hispidus* have anterior cingulids on m2 and m3, *S. libitinus* lacks these cingulids on most but not all teeth, and *S. bakeri* completely lacks anterior cingulids. Size is also an important diagnostic character used to separate the various species of *Sigmodon*. *S. medius* and *S. minor* are both quite small, and in fact these two species are often synonymized under *S. minor*. *S. curtisi*, *S. libitinus*, and *S. bakeri* are intermediate in size, with *S. curtisi* slightly larger than the other two. *S. hispidus* is the largest species of the genus in Florida. Measurements of the mandible and lower dentition

of fossil and modern *Sigmodon* from Florida are presented in Table 6. Although not extensive, the sample of lower molars of *Sigmodon* from Leisey is adequate for relatively detailed comparisons with other extinct and living species of the genus from Florida (Figs. 6A-B).

Sigmodon medius can easily be separated from the Leisey *Sigmodon* by its smaller size, lack of accessory roots on m1, and lower crowned teeth. *S. minor*, known from Florida only by two teeth from the De Soto Shell Pit, is so much smaller than the Leisey *Sigmodon* that further comparisons are unnecessary. *S. curtisi* from Inglis differs from the Leisey cotton rat in its larger size, much greater frequency of anterior cingulids on m2 and m3, and nearly symmetrical anteroconid on m1. *S. bakeri* can be separated from the Leisey *Sigmodon* by the presence of a fourth lingual accessory root on m1 and by the more prominent posterolabial extension of the anteroconid. The extant cotton rat, *S. hispidus*, represents the most advanced species of the genus, and can be distinguished from the Leisey *Sigmodon* by its larger size, presence of two accessory roots on m1, presence of well developed anterior cingulids on m2 and m3, and higher crowned teeth.

The Leisey *Sigmodon* compares quite well in most respects with the sample of *S. libitinus* from Haile 16A, the type locality of this species (Martin 1979). The Leisey sample is very similar in size to both *S. libitinus* and *S. bakeri* (Table 6). Nine of ten m1s from Leisey have three roots, including large anterior and posterior roots and a much smaller labial accessory root. Only a single m1 from Leisey (UF 128974) has a tiny fourth lingual accessory root. Similarly, only two of twenty m1s (10%) of *S. libitinus* from Haile 16A possess the minuscule fourth lingual accessory root. All Leisey m1s have asymmetrical anteroconids, most of which have small to moderately developed posterolabial extensions as in the Haile 16A sample. An anterior cingulid is absent from all seven m2s in the Leisey sample and is present on only one of five m3s (UF 128977; Fig. 6B). However, many of the lower molars from Leisey are well worn and the anterior cingulid is generally only in evidence on unworn to lightly worn teeth. About half of the 20 mandibles of *S. libitinus* examined from Haile 16A have small to moderately well developed anterior cingulids on m2 and m3.

The Leisey *Sigmodon* is very similar in size and most dental features to *S. libitinus*, and is here confidently referred to that species. The only character in which the Leisey *Sigmodon* differs from the type series of *S. libitinus* from Haile 16A is the higher incidence of anterior cingulids on m2 and m3 in the Haile 16A sample. The rarity of anterior cingulids in the Leisey teeth is a character shared with the late Irvingtonian species *S. bakeri*. This difference may indicate a slightly younger age for Leisey compared to Haile 16A, but is not a significant enough feature to warrant description of a new species.

In many respects, *S. libitinus* from Haile 16A and Leisey is intermediate between *S. curtisi* from Inglis 1A and *S. bakeri* from Coleman 2A. *S. libitinus* agrees with *S. curtisi* in the possession of only three roots on m1, but is similar to

Table 6. Measurements (in mm) of the mandible and lower dentition of fossil and Recent *Sigmodon* from Florida. Mean, observed range, and sample size, respectively, are provided for each measurement.

Species, Locality, and Age	Alveolar length of mandibular toothrow	length		width		width	
		m1	m1	m2	m2	m3	m3
<i>Sigmodon curtisi</i>							
Inglis 1A	6.62	2.37	1.65	1.76	1.86	2.28	1.76
earliest	6.33-6.78	2.20-2.51	1.56-1.75	1.65-1.82	1.75-2.00	2.03-2.45	1.66-1.85
Irvingtonian	10	10	10	10	10	7	7
<i>Sigmodon libitinus</i>							
Haile 16A	6.19	2.26	1.54	1.60	1.71	2.12	1.65
late early	5.87-6.52	2.13-2.37	1.48-1.63	1.53-1.69	1.61-1.77	1.86-2.27	1.53-1.74
Irvingtonian	10	10	10	10	10	10	10
<i>Sigmodon libitinus</i>							
Leisey Shell Pit	6.03	2.20	1.49	1.59	1.65	1.92	1.65
late early	5.93, 6.12	2.04-2.32	1.42-1.56	1.51-1.65	1.56-1.71	1.80-2.01	1.52-1.77
Irvingtonian	2	8	9	7	7	3	3
<i>Sigmodon bakeri</i>							
Coleman 2A	6.03	2.23	1.52	1.55	1.69	1.87	1.59
late Irvingtonian	5.80-6.35	2.05-2.53	1.46-1.58	1.46-1.68	1.60-1.81	1.84-1.90	1.51-1.70
	8	12	12	7	7	3	3
<i>Sigmodon hispidus</i> ¹							
Reddick 1A	7.27	2.49	1.73	1.82	2.02	2.59	1.88
late	6.83-7.65	2.24-2.72	1.63-1.86	1.67-1.95	1.88-2.14	2.24-3.00	1.77-1.96
Rancholabrean	18	18	18	18	18	18	18
<i>Sigmodon hispidus</i> ¹							
Recent, Florida	7.26	2.47	1.65	1.77	1.97	2.56	1.91
	6.56-7.80	2.11-2.73	1.55-1.88	1.59-1.96	1.79-2.13	2.17-2.89	1.77-2.10
	30	30	30	30	30	30	30

¹ Measurements from Martin (1979, Table 1).

S. bakeri in size and in the asymmetrical structure of the anteroconid on m1. The *S. libitinus* sample from Haile 16A is similar to *S. curtisi* in having small anterior cingulids in about half of the lower m2s and m3s. The Leisey sample seems to be more similar to *S. bakeri* in lacking the anterior cingulids in the majority of the second and third lower molars. No anterior cingulid was observed in any specimens of *S. bakeri* examined.

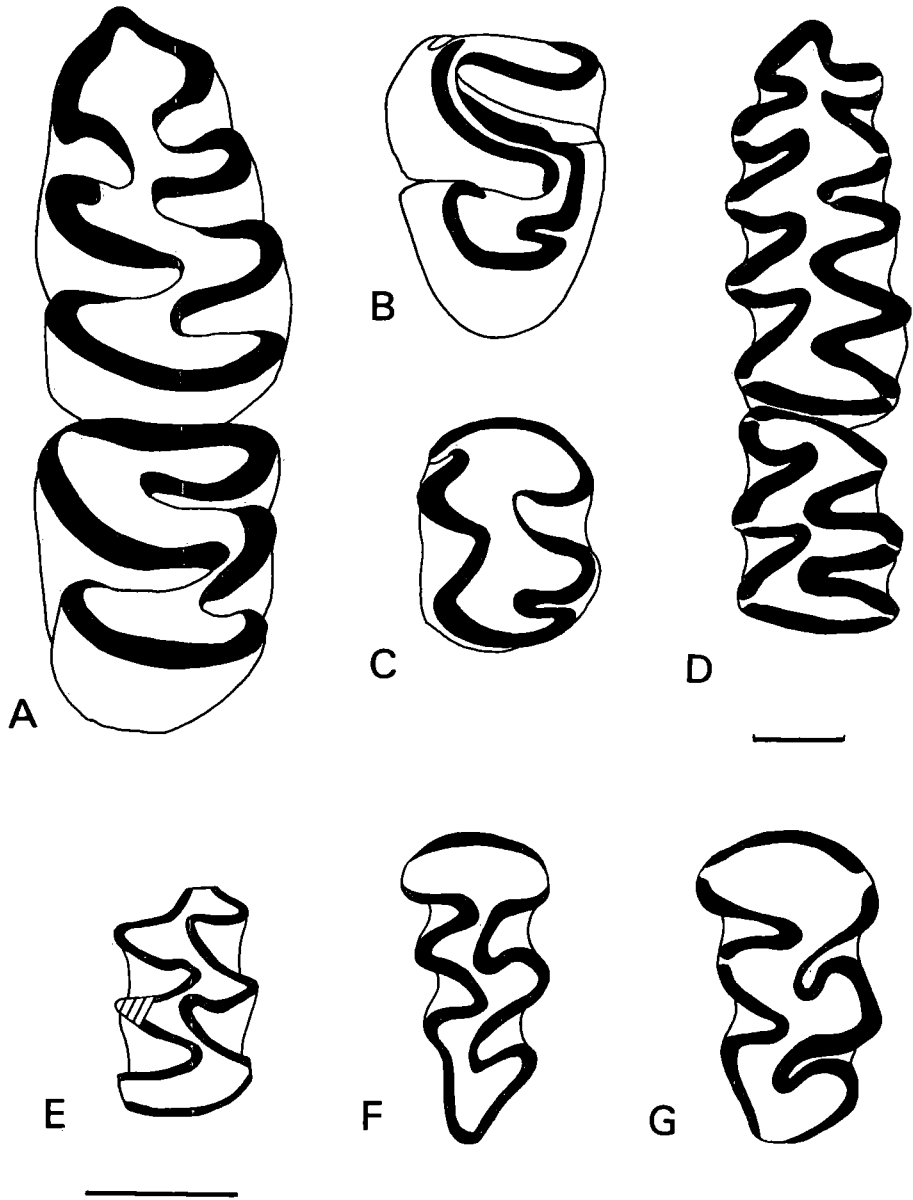


Figure 6. (A) *Sigmoidon libitinus*, Leisey 3A, left m1-m2, UF 124587; (B) *Sigmoidon libitinus*, Leisey 3A, left m3, UF 128977.; (C) *Podomys* sp., Leisey 3A, left m2, UF 124332; (D) *Ondatra annectens*, Leisey 3, left m1-m2, UF 125207; (E) *Pedomys* sp., Leisey 3A, right m2, UF 124334; (F) *Pedomys* sp., Leisey 3A, right M3, UF 125170; (G) *Pedomys* sp., Leisey 3A, right M3, UF 125212. Both scale bars 1 mm in length, shorter scale applies only to D, longer scale applies to A-C and E-G.

Sigmodon libitinus is also present in two other Florida early Irvingtonian sites. A left mandible with m1-m3 (UF 91014) was collected by James Ranson from the Shell Materials Pit located in Ruskin, Hillsborough County, only about 5 km north of Leisey. This specimen is very similar in size and other morphological features to the *S. libitinus* sample from Leisey, with one exception. The nearly unworn m2 and m3 of this mandible have small but readily discernible anterior cingulids. A fourth sample of *S. libitinus* from the early Irvingtonian Payne Creek Mine in Polk County consists of a maxilla with two teeth, a mandible with two teeth, and seven isolated molars. The Payne Creek *Sigmodon* sample contains four m1s (UF 129026, 129028-129030) that are nearly identical to those from Leisey. Three of these four teeth have three roots, while the fourth has a tiny fourth lingual accessory root. All four Payne Creek m1s have a rather well developed posterolabial extension on the anteroconid. A nearly unworn m2 (UF 129031) from Payne Creek has a tiny anterior cingulid that obviously would have disappeared with only moderate wear. A well worn m2 and m3 in a mandible (UF 129032) lack any evidence of an anterior cingulid, as is typical of the Leisey sample.

Remarks.—Cotton rats of the genus *Sigmodon* are usually the most abundant small mammals in Florida Irvingtonian faunas. The various species of *Sigmodon* in Florida apparently filled the ecological role of small grazing rodents that is typically occupied by arvicolines in more temperate northern and western faunas (Martin 1979). In his review of the evolutionary history of *Sigmodon*, Martin (1979) noted that the replacement chronology of *Sigmodon* species in the Plio-Pleistocene of Florida provides a very useful biochronological sequence. Identification of a *Sigmodon* species from a Florida site permits chronologic refinement to a portion of a NALMA. Whereas arvicoline rodents are generally rare or absent in Florida Blancan and Irvingtonian sites, *Sigmodon* is usually present if a site has any small mammals at all. Furthermore, it is not necessary to have a large sample; a single mandible or even an isolated m1 of *Sigmodon* may be adequate for a species identification.

Six species of cotton rats are recorded from faunas in Florida starting in the late Blancan and continuing until the present. 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). *S. medius* is the characteristic cotton rat of the Blancan NALMA. *S. medius* was originally described from the Benson LF of Arizona, and has since been reported from numerous Blancan faunas throughout the western United States (Kurtén and Anderson 1980). *S. medius* is unknown from faunas younger than late Blancan, unless this species is synonymized with *S. minor*, in which case its chronological range extends into the earliest Irvingtonian. *S. minor* is here reported from Florida for the first time in the earliest Irvingtonian De Soto Shell Pit LF. The two teeth of *S. minor* from De

Soto are much smaller than comparable teeth of *S. medius* from the older Haile 15A and Macasphalt Shell Pit local faunas.

The De Soto Shell Pit is the only Florida fossil site with two species of *Sigmodon*, as *S. curtisi* occurs there as well. *S. curtisi* was first recorded in Florida from the earliest Irvingtonian Inglis 1A by Martin (1979). Western faunas containing *S. curtisi* are the Curtis Ranch LF in Arizona (type locality) and the correlative Vallecito Creek LF in California, as well as the slightly younger Kentucky LF in Kansas (Martin 1979). Winkler and Grady (1990) also mentioned the presence of *S. curtisi* in the Fyllan Cave LF in Texas, which may be as young as middle Irvingtonian. *S. libitinus* previously was restricted to the type locality, the early Irvingtonian Haile 16A LF (Martin 1979). *S. libitinus* is now known from the Leisey Shell Pit, the Payne Creek Mine LF, and the Shell Materials Pit, all of which are roughly correlative late early Irvingtonian faunas. *S. bakeri* was described from the late Irvingtonian Coleman 2A LF (Martin 1974, 1979), and also was reported from several Florida early Rancholabrean local faunas, including Bradenton, Haile 7A, and Williston 3A. The extant cotton rat *S. hispidus* is the typical species found in Florida late Rancholabrean faunas, although it first appears in the early Rancholabrean Haile 8A and Daytona Beach local faunas.

Podomys sp.

Referred Specimen.—Leisey 3A: UF 124332, left m2. MNI=1.

Description.—A single well worn m2 is the only specimen of a peromyscine rodent recovered from the Leisey Shell Pit LF (Fig. 6C). We follow Carleton's (1980) classification in which he recognized many former subgenera of *Peromyscus*, including *Podomys*, as full genera. The Leisey tooth agrees in general morphological characters with modern species of peromyscines from Florida, including the cotton mouse *Peromyscus gossypinus* and the Florida mouse *Podomys floridanus*. However, this tooth is far larger than *Peromyscus gossypinus* and somewhat larger than *Podomys floridanus*. The dimensions of the Leisey m2 are: length 1.74 mm, width 1.34 mm. Measurements of ten m2s of modern *Podomys floridanus* from Alachua County, Florida are: length (mean=1.38, range=1.34-1.43), width (mean=1.16, range=1.12-1.20). The large size of the Leisey tooth is notable, as *P. floridanus* is one of the largest living species of peromyscines in the United States.

Only two Irvingtonian species of *Peromyscus* (*sensu lato*) appear to be within the size range of the large Leisey tooth, *P. cumberlandensis* and *P. irvingtonensis*. *P. cumberlandensis* was originally described from the middle Irvingtonian Cumberland Cave LF in western Maryland (Guilday and Handley 1967). This species also has been reported from the middle Irvingtonian Trout Cave LF in West Virginia and the Rancholabrean Ladds Quarry in northern Georgia (Ray

1967). Measurements of nine m2s of *P. cumberlandensis* from Cumberland Cave are (from Guilday and Handley 1967): length (mean=1.7, range=1.6-1.8); width (mean=1.4, range=1.3-1.5). The average size of the Cumberland Cave m2s is almost exactly the same as the Leisey tooth. Guilday and Handley (1967) described *P. cumberlandensis* as having a moderately complicated dental pattern with relatively well developed mesolophids and mesostylids on the lower molars. However, they also noted that the mesolophid and mesostylid were present in only 33% of the m2s in the Cumberland Cave sample. The Leisey tooth has a comparatively simple dental pattern. A mesolophid is absent and the mesostylid and ectostylid are present, but both cusps are very small, especially the mesostylid. Because the mesolophid and mesostylid are present on only one-third of the *P. cumberlandensis* m2s, the Leisey specimen cannot definitely be excluded from this species, although it is unlikely that the two taxa are conspecific. Savage (1951) described *Peromyscus irvingtonensis* based on a single mandible lacking m2 from the type Irvington fauna in California. This large species is a member of the primitive subgenus *Haplomyomys*, which is characterized by the absence of accessory cusps on the molars. As noted above, the Leisey tooth has two very small accessory cusps, a mesostylid and ectostylid.

A third, large extinct species of *Peromyscus*, *P. oklahomensis*, occurs in two early Rancholabrean faunas, the Doby Springs LF from Oklahoma and the Easley Ranch LF in Texas. The type specimen of *P. oklahomensis* from Doby Springs is an m2. The measurements of this tooth are: length 1.7 and width, 1.3, exactly the same dimensions as the Leisey m2. Furthermore, *P. oklahomensis* was described as having a simple dental pattern resembling that of the slightly smaller Florida mouse, *Podomys floridanus*. However, based on the diagnosis and figure (Stephens 1960), *P. oklahomensis* differs in several characters from the Leisey tooth, including the very broad reentrant valleys between the major cusps, a well developed mesostylid, and reduced ectostylid. In the Leisey specimen, the cusps are separated by rather narrow re-entrant valleys and the ectostylid is larger than the mesostylid, although both cusps are rudimentary.

It appears likely that the Leisey peromyscine m2 represents a large, undescribed species of *Podomys*. However, a single worn tooth is inadequate for the description of a new species. No morphological characters other than larger size clearly distinguish the Leisey m2 from modern comparative specimens of *Podomys floridanus* from peninsular Florida. In a sample of ten m2s of *P. floridanus*, a mesolophid is absent from all ten teeth, six teeth have a small mesostylid, and eight have a small ectostylid. The Leisey m2 lacks a mesolophid and bears a small mesostylid and ectostylid.

Undescribed specimens of large peromyscines are present in other Florida Irvingtonian faunas. A nearly complete mandible with m1-m3 from the early Irvingtonian Haile 21A LF (UF 62638) is larger than *P. floridanus*, but the m2 is smaller than the Leisey tooth (measurements: length 1.61, width 1.27). Furthermore, the Haile 21A m2 has a small mesolophid, a character that is absent

in *P. floridanus* and the Leisey specimen. An upper M2 of a large peromyscine from the early Irvingtonian Payne Creek Mine LF (UF 129023) cannot be directly compared to the Leisey tooth, but was compared to the extant *P. floridanus* sample. The Payne Creek tooth has a well developed mesoloph, a feature lacking in *P. floridanus*. The best sample of large peromyscines from the Florida Irvingtonian is found in the Haile 16A LF. Detailed analysis of this sample is beyond the scope of the present study; however, a preliminary examination suggests that the large Haile 16A peromyscine has a simple dental pattern and is probably referable to *Podomys*. The Haile 16A and Leisey *Podomys* are very similar, if not conspecific.

Subfamily ARVICOLINAE Gray 1821

Ondatra annectens (Brown 1908)

Referred Specimen.—Leisey 3: UF 125207, left mandible with i1, m1-m2. MNI=1.

Description.—A single well preserved mandible with a partial incisor and complete m1 and m2 is the only specimen of *Ondatra* recovered from the Leisey Shell Pit (Fig. 6D). The presence of *Ondatra* in the Leisey fauna is certainly fortuitous, as the evolutionary history of the muskrat lineage is perhaps better known than that of any other rodent in the Plio-Pleistocene of North America (Semken 1966; Nelson and Semken 1970; Martin and Tedesco 1976). The morphological characters used to distinguish the various species in the lineage consist primarily of features evident on the m1, including size (length and width), number of triangles, complexity of the anteroconid, amount of cement in the reentrant angles, and height of the dentine tracts. The only one of these characters not readily observable in the Leisey mandible is the height of the dentine tracts on m1, as both teeth are firmly implanted in the mandible. However, some of the dentine tracts on m1 reach the occlusal surface of the tooth and this, taken in conjunction with the wear stage, does provide a good approximation of dentine tract height.

Measurements of the total length and maximum width of the occlusal surface of m1 are presented in Table 7 for five samples of *Ondatra* from Florida: *O. idahoensis* from the earliest Irvingtonian Inglis 1A and De Soto Shell Pit local faunas, *O. annectens* from the early Irvingtonian Leisey Shell Pit and Payne Creek Mine local faunas, and *O. zibethicus* from the late Rancholabrean Ichetucknee River LF. Two of these sites, De Soto and Leisey, are represented by a single specimen. The sample of *O. idahoensis* from Inglis 1A is one of the largest known for this species, including 20 mandibles, 12 of which have an m1. The Payne Creek sample of *O. annectens* includes three complete m1s, as well as eight additional isolated teeth. The four Florida Irvingtonian samples fit rather well into the two typical late Pliocene and early Pleistocene species of *Ondatra* described

from western North America, *O. idahoensis* from the late Blancan and earliest Irvingtonian and the somewhat larger *O. annectens* from the late early and middle Irvingtonian.

The measurements of the *Ondatra* m1 from the Leisey Shell Pit and three m1s from Payne Creek Mine (Table 7) are within the size range of *O. annectens* (Nelson and Semken 1970). Comparison with the oft-cited figure in Nelson and Semken (1970, fig. 1), which shows the ratio of length to width in the m1 of the classic Blancan through Rancholabrean *Ondatra* samples from North America, demonstrates that the Leisey and Payne Creek Mine *Ondatra* falls well within the range of *O. annectens* from the early Irvingtonian Java LF from South Dakota and Kentuck LF from Kansas and the middle Irvingtonian Cudahy LF in Kansas. Twelve m1s of *Ondatra* from Inglis 1A and one m1 from the De Soto Shell Pit are notably smaller than m1s from Leisey and Payne Creek (Table 7). The Inglis and De Soto *Ondatra* compare well in length with samples of *O. idahoensis* from the late Blancan Grandview LF in Idaho and White Rock LF in Kansas. However, the Florida *O. idahoensis* are narrower than western specimens of similar age, averaging less than 2.0 mm, while all of the western *O. idahoensis* samples average greater than 2.0 mm in width (ranging from 2.1-2.4 mm). A sample of 23 m1s of *O. zibethicus* from the late Rancholabrean Ichetucknee River LF in Columbia County (Table 7) is considerably larger than *O. annectens*.

Ondatra annectens has five to seven closed triangles on the m1. The presence of five triangles is a primitive feature in the muskrat lineage and is typical of all species prior to *O. annectens*, including *O. idahoensis*, while *O. zibethicus* usually has seven or more closed triangles. The Leisey m1 has six closed triangles on m1, as well as a broadly open, rudimentary seventh triangle. All three m1s from the Payne Creek Mine have only five closed triangles, but small open sixth and seventh triangles are present. The pattern of enamel triangles on the m1 from these two sites is actually very similar. The only difference is that in the Leisey m1 the fourth lingual reentrant extends almost entirely across the tooth and nearly contacts the fourth labial reentrant, thereby isolating a sixth triangle. The fourth lingual reentrant in the Payne Creek sample does not extend as far labially, and thus the sixth triangle, although well developed, is not closed. In a sample of *O. annectens* from the Java LF (Martin 1989), unworn m1s may have as many as seven well separated triangles, while deeply worn specimens usually have only five closed triangles with rudimentary sixth and seventh triangles, as in the Payne Creek *O. annectens*.

The m1s of *Ondatra annectens* from Leisey and Payne Creek have five lingual and four well developed labial reentrants, whereas *O. idahoensis* typically possesses five lingual, but only three large labial reentrants. In the m1 from De Soto Shell Pit and most of the specimens from Inglis 1A there are also one to two tiny labial reentrants on the anteroconid. The larger and more posterior of these

Table 7. Measurements (in mm) of the m1 of fossil *Ondatra* from Florida. Mean, observed range, and sample size, respectively, are provided for the samples from Inglis 1A, Payne Creek Mine, and Ichetucknee River.

Species and Locality	length m1	width m1
<i>Ondatra idahoensis</i> Inglis 1A	4.5 (4.2-4.8) N=12	1.9 (1.7-2.1) N=10
<i>Ondatra idahoensis</i> De Soto Shell Pit UF 125222	4.6	1.9
<i>Ondatra annectens</i> Leisey Shell Pit UF 125207	5.6	2.5
<i>Ondatra annectens</i> Payne Creek Mine	5.8 (5.5-6.0) N=3	2.5 (2.4-2.6) N=3
<i>Ondatra zibethicus</i> Ichetucknee River	7.7 (7.3-8.3) N=23	2.9 (2.6-3.2) N=23

two rudimentary reentrants is probably homologous with the prominent fourth labial reentrant of *O. annectens*.

When comparing teeth of similar wear stage, the dentine tracts are much better developed and extend higher on the m1 in *Ondatra annectens* from Leisey and Payne Creek than in *O. idahoensis* from De Soto and Inglis. On the Leisey m1, the dentine tracts extend to the occlusal surface on the lingual and labial termination of all triangles except one, as well as on the posterior loop. The Leisey tooth is moderately worn, but not extremely so. The dentine tracts in the three m1s from Payne Creek are similar in their development to the Leisey specimen. In a deeply worn m1 from Payne Creek all dentine tracts reach the occlusal surface, whereas in a lightly worn tooth only about half of the dentine tracts intersect the tooth crown. In the third Payne Creek tooth all but one of the labial and lingual reentrants reach the occlusal surface, just as in the Leisey specimen. The dentine tracts are not nearly so well developed in the *O. idahoensis* sample from Inglis and De Soto. Not a single dentine tract reaches the occlusal surface in the De Soto tooth, while in the Inglis 1A sample the dentine tracts fail to reach the occlusal surface in seven m1s. On the remaining five teeth, most of which are more heavily

worn, a single dentine tract located at the labial termination of the posterior loop extends to the tooth crown.

Both *Ondatra annectens* and *O. idahoensis* are characterized by the presence of cement in the reentrant angles; however, the cement is much better developed in the former species. From one-half to three-fourths the width of the reentrant angles is filled with cement in the Leisey and Payne Creek *O. annectens* m1s. Although cement is present in all reentrant angles of the m1 in the two Florida *O. idahoensis* samples, it often consists of a thin layer, generally filling less than one-fourth the width of the reentrant.

The anterior half of a lightly worn m1 (UF 11455) from the Pool Branch LF in Polk County constitutes a third record of *Ondatra annectens* from Florida. The fourth lingual reentrant in the Pool Branch m1 extends almost entirely across the tooth, but does not quite contact the fourth labial reentrant, and thus the sixth triangle is not completely closed. Dentine tracts reach the occlusal surface at the labial and lingual termination of four of the five triangles preserved, and cement fills about three-fourths the breadth of the reentrant angles. Although incomplete, the *Ondatra* m1 from Pool Branch is similar in size and dental characters to *O. annectens* from Leisey and the nearby Payne Creek Mine.

Remarks.—The phyletic lineage of North American muskrats has been variously interpreted as containing six species in two genera (from oldest to youngest: *Pliopotamys minor*-*P. meadensis*-*Ondatra idahoensis*-*O. annectens*-*O. nebracensis*-*O. zibethicus*) to consisting of a single continuously evolving lineage placed in the extant species *Ondatra zibethicus* (Martin 1993). Early and middle Blancan faunas and the muskrats typical of this time period, the two species of *Pliopotamys*, are unknown from Florida. However, three of the four species of *Ondatra* known from Irvingtonian and Rancholabrean faunas have been identified from Florida. Only *O. nebracensis* is unrecorded from the state.

Species of *Ondatra* are excellent biochronological indicators in Irvingtonian and Rancholabrean faunas throughout North America (Nelson and Semken 1970; Martin and Tedesco 1976). *Ondatra* is uncommon in Florida late Pliocene and Pleistocene vertebrate faunas, but when present provides a good indication of the age of a site. The oldest arvicoline rodent known from Florida is *O. idahoensis* from the latest Pliocene Inglis 1A and De Soto Shell Pit local faunas. Frazier (1981) first noted the presence of *O. idahoensis* at Inglis 1A. The Inglis muskrat was previously reported as *O. zibethicus* (Webb 1974). Numerous other mammalian taxa in common between Inglis and De Soto indicate that these faunas are earliest Irvingtonian in age. *O. idahoensis* also occurs in the earliest Irvingtonian Curtis Ranch LF in Arizona (Irvingtonian I of Repenning 1987), as well as slightly older late Blancan faunas (Blancan V of Repenning 1987), including Borchers and White Rock in Kansas, Mullen and Seneca in Nebraska, and Grand View in Idaho (type locality).

The larger and more advanced muskrat, *O. annectens*, is here reported from the Leisey Shell Pit, as well as the early Irvingtonian Pool Branch and Payne Creek local faunas from the Bone Valley Region in Polk County. These three sites have similar mammalian faunas that are late early Irvingtonian in age (Morgan and Hulbert this volume). *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 faunas similar in age to Leisey that contain *O. annectens* include: Java, South Dakota (Martin and Tedesco 1976; Martin 1989); Kentuck and Wathena, Kansas (Repenning 1987; Martin in press); and Sappa, Nebraska (Martin and Schultz 1985). *O. annectens* occurs in many middle Irvingtonian faunas as well, including: Conard Fissure, Arkansas (type locality); Cudahy, Kansas; Vera, Texas; and Cumberland Cave, Maryland.

Prior to the relatively recent discovery of *Ondatra idahoensis* and *O. annectens* in Florida Irvingtonian faunas, the only fossils of *Ondatra* known from the state were late Pleistocene specimens of the living species, *O. zibethicus*. Lawrence (1942) described the large extinct subspecies, *O. zibethicus floridanus*, from the late Rancholabrean Ichetucknee River LF in Columbia County in northern peninsular Florida. Since then *O. zibethicus* has been identified from six other late Rancholabrean local faunas in northern Florida, four in the peninsula and two in the eastern panhandle. The southernmost Florida record of *O. zibethicus* is from the Withlacoochee River 7A LF on the border between Citrus and Levy counties. All Florida localities containing *O. zibethicus* appear to have sampled freshwater depositional environments, including six river-bottom sites and Devils Den in Levy County, the latter a water-filled sinkhole/cave complex. *O. zibethicus* is no longer found in Florida where it is replaced by the round-tailed muskrat, *Neofiber alleni*. The closest extant populations of *O. zibethicus* are found in southern Georgia and southern Alabama less than 100 km from the Florida border (Hall 1981). *O. zibethicus* also has been reported from an archaeological site approximately 2500 years old from Jackson County in the panhandle (Neill and Bullen 1955).

Pedomys sp.

Referred Specimens.--Leisey 1A: UF 121913, 131999, left M1 (2). Leisey 3A: UF 125169, right M1; UF 124333, left M2; UF 125170, 125212, right M3; UF 125171, posterior half of left m1; UF 124334, right m2. MNI=4.

Description.--Eight teeth from Leisey are referred to a new species of *Pedomys*, currently being described from the Haile 16A LF by Robert Martin (in press), who has generously allowed me to use his descriptions and measurements of this new species. Martin included *Pedomys* as a subgenus of *Microtus*, but we prefer to treat *Pedomys* as a distinct genus. *Pedomys* includes the living species *P.*

ochrogaster, along with several fossil forms. It is unfortunate that the Leisey *Pedomys* sample does not include a complete m1, the most diagnostic tooth in arvicoline rodent systematic analysis. A partial m1 from Leisey 3A (UF 125171) has the posterior loop and two triangles, but several additional triangles and the anteroconid are missing. Although not complete enough for standard measurements, comparisons indicate that the Leisey m1 is larger than the m1 of the extant pine vole, *Pitymys pinetorum*, and is similar in size to the new *Pedomys* from the early Irvingtonian Haile 16A LF.

A single complete m2 of *Pedomys* (UF 124334) is present in Leisey (Fig. 6E). According to Martin (in press), the third and fourth triangles of m2 are closed in 9 of 26 specimens (35%) of the Haile 16A *Pedomys*. The Leisey m2 has the third and fourth triangles closed. The anterior width of the Leisey tooth is 1.02 mm, which is exactly the mean anterior width of 15 m2s of *Pedomys* from Haile 16A (Martin in press). Overall, the m2s of the undescribed *Pedomys* from Haile 16A and Leisey are larger and have a narrower dentine isthmus between the third and fourth triangles than the m2 of the living prairie vole, *P. ochrogaster* (Martin in press).

The M1 and M2 of the Haile 16A *Pedomys* are typical for the genus, but are not particularly useful for further differentiating the species. This is unfortunate since four of the eight teeth comprising the Leisey *Pedomys* sample are either M1 or M2. The Leisey sample does contain two complete M3s (Figs. 6F-G), which is generally regarded as the next most diagnostic tooth after the m1. Measurements of the Leisey M3s are (in mm): anteroposterior length (2.06, 2.32) and anterior width (1.15, 1.17). The Leisey teeth are similar in dental pattern to the M3 of the Haile 16A *Pedomys*; however, both Leisey M3s lack cement in the 4th lingual and 3rd labial reentrants. In the Haile 16A sample, 79% of the M3s have the 4th lingual reentrant filled with cement and 29% have the 3rd labial reentrant filled with cement (Martin in press).

An unreported sample of *Pedomys* that includes three complete m1s is present in the early Irvingtonian Payne Creek LF. The anteroposterior length of the three Payne Creek m1s (3.26, 3.36, 3.48) is well within the size of the undescribed Haile 16A *Pedomys* (mean 3.11 mm, range 2.73-3.52, sample size 27; measurements from Martin in press), although the mean of the Payne Creek sample (3.37) is somewhat larger. Like the Haile 16A sample, the Payne Creek *Pedomys* m1s are larger than most other closely related Irvingtonian species, including *Allophaiomys pliocaenicus* from Java in South Dakota and Kentuck and Wathena in Kansas, and *Pedomys* (or *Allophaiomys*) *guildayi* from Cumberland Cave, Maryland. Similarity in size and dental features suggests that *Pedomys* samples from Leisey Shell Pit, Payne Creek Mine, and Haile 16A belong to the same species.

Remarks.— The undescribed species of *Pedomys* from Haile 16A (Martin in press), Leisey Shell Pit, and Payne Creek Mine represents the earliest member of

the genus in Florida. Moreover, these three early Irvingtonian samples appear to be among the earliest records of either *Pedomys* or *Pitymys* in North America, although this point strongly hinges on the definition of these two genera (see discussion in Martin [1987] and Repenning and Grady [1988]). The oldest prior record of this arvicoline group in Florida was the large extinct species *Pitymys aratai* described from the late Irvingtonian Coleman 2A LF (Martin 1974).

There is now a rather well documented chronology of *Pedomys* and *Pitymys* species in Florida Irvingtonian and Rancholabrean sites, although there are still some gaps. According to Martin (in press), the *Pedomys/Pitymys* replacement chronology provides an excellent indicator of age for the Florida sites in which species of this group occur. Four species are known from successively younger sites in Florida. The earliest species currently being described by Martin (in press) occurs in late early Irvingtonian sites ranging in age from 1.6 to 1.0 Ma, including Haile 16A, Leisey Shell Pit, and Payne Creek Mine. This species may be derived from *Allophaiomys*, a typical early Irvingtonian arvicoline genus known from both eastern and western North America (Martin 1987, in press). L. D. Martin (1989) noted that the earliest North American records of the *Microtus* (*sensu lato*) radiation, in particular the genus *Allophaiomys*, are from the early Irvingtonian. *Allophaiomys* occurs in a number of early Irvingtonian faunas considered to be correlatives of Leisey, including Java, Kentuck, Wathena, and Sappa as well as the somewhat older earliest Irvingtonian Wellsch Valley LF in Saskatchewan and the younger middle Irvingtonian Hamilton Cave LF in West Virginia (Repenning and Grady 1988).

After the early Irvingtonian there is a gap encompassing the middle Irvingtonian where *Pedomys* and *Pitymys* are unknown from Florida, although only one major Florida site, the McLeod Limerock Mine LF, occurs during this interval. The large species *Pitymys aratai* is known only from the Irvingtonian Coleman 2A LF (Martin 1974). Florida early Rancholabrean faunas, including Williston 2A (type locality) and Bradenton, are characterized by *Pitymys hibbardi* (see Martin 1974). The extant species *Pitymys pinetorum* does not appear in the Florida fossil record until the late Rancholabrean.

Synaptomys sp.

Referred Specimens.--Leisey 3A: UF 121914, partial left M2; UF 125172, left m3. MNI=1.

Remarks.--Two teeth from Leisey 3A are identified as *Synaptomys* sp. The only other Irvingtonian site in Florida containing *Synaptomys* is the early Irvingtonian Haile 16A LF (Martin in press). The Leisey teeth were compared to modern specimens of *S. cooperi*, as well as to fossil teeth of *S. australis* from the Rancholabrean Reddick 1A LF, Marion County, Florida and the *Synaptomys* from

Haile 16A. *S. australis* is similar in dental morphology to *S. cooperi*, but is much larger. Like *S. australis*, the Leisey *Synaptomys* teeth are distinctly larger than comparable teeth of *S. cooperi*. The Leisey teeth are very similar in size and other dental characters to the bog lemming teeth from Haile 16A. The large *Synaptomys* from Haile 16A is related to *S. australis* according to Martin (in press), but only further study of the Haile fossils will determine whether this sample represents *S. australis* or an undescribed species. The final identification of the Leisey teeth must await detailed analysis of the larger sample from Haile 16A.

The early Irvingtonian records of *Synaptomys* from Leisey and Haile 16A represent by far the oldest bog lemmings from Florida. Previously published records of *Synaptomys* from the state are restricted to Rancholabrean sites, all of which have been referred to *S. australis* (Simpson 1928; Olsen 1958). The oldest Florida record of *S. australis* is from the early Rancholabrean Bradenton LF. This species also has been reported from Rancholabrean sites in Texas and Kansas (Kurtén and Anderson 1980).

The genus *Synaptomys* is used here in the restricted sense of Repenning and Grady (1988) to include only the extant southern bog lemming *S. cooperi* and the extinct Florida bog lemming *S. australis*. Some authors (e.g. Kurtén and Anderson 1980; Repenning and Grady 1988) have suggested that *S. australis* represents a large, extinct southern subspecies of *S. cooperi*, a living species currently found no farther south than the Appalachian Mountains of Tennessee and North Carolina (Hall 1981). The earliest records of *S. cooperi* are from middle Irvingtonian faunas, including Fyllan Cave in Texas (Taylor 1982; Repenning and Grady 1988), Cumberland Cave, and Trout Cave. Rancholabrean records of *S. cooperi* from outside the species' current range are known from sites in Georgia, Texas, and northern Mexico (Kurtén and Anderson 1980). Until more detailed comparisons are made between *S. cooperi* and the large Rancholabrean samples of *S. australis* from Florida, we tentatively recognize the latter species.

DISCUSSION

Over the past two decades numerous Irvingtonian vertebrate faunas have been discovered in Florida, and it is now one of the most densely sampled geographic regions in North America for faunas representing the Irvingtonian NALMA. Prior to the present volume on the Leisey Shell Pit, the only other Florida Irvingtonian mammalian fauna to be comprehensively studied was the late Irvingtonian Coleman 2A LF (Martin 1974). Webb (1974) presented mammalian faunal lists and brief site descriptions for three other Florida Irvingtonian sites: Inglis 1A, Pool Branch, and Punta Gorda. Coleman 2A, Inglis 1A, Pool Branch, and Punta Gorda were the only Irvingtonian sites from Florida listed by Kurtén and Anderson (1980). Lundelius et al. (1987) placed Inglis 1A and Coleman 2A, as well as the

Haile 16A LF from Alachua County, on their correlation chart of North American Plio-Pleistocene faunas.

The small mammal fauna from the Leisey Shell Pit is not abundant or diverse compared to those of Inglis 1A, Haile 16A, and Coleman 2A. However, there are enough diagnostic taxa of rodents and lagomorphs from Leisey to make meaningful biochronological comparisons with similar taxa from other Irvingtonian faunas in Florida and elsewhere (see Table 8). The rarity of small mammals at Leisey 1A is probably related to the estuarine or coastal depositional environment of this site. The influences of fluvial transport and tides likely led to the winnowing out or destruction of most small mammal bones from the Leisey 1A deposit. The quiet freshwater environmental setting of Leisey 3A was more suitable for the preservation of freshwater and terrestrial microvertebrates.

Besides the three orders of small mammals recorded from Leisey, two other orders, the Marsupialia and Chiroptera, are known from other Florida Irvingtonian sites. The latest Irvingtonian Coleman 2A LF represents the earliest North American record of the opossum (Martin 1974), *Didelphis virginiana*, a species otherwise restricted to the Rancholabrean and Recent in Florida and elsewhere. Bats are often abundant in Florida cave and fissure deposits. Seven species of bats have been identified from the earliest Irvingtonian Inglis 1A LF (Morgan 1991), three species are known from Coleman 2A (Martin 1974), and two each occur in Haile 16A and Haile 21A (Morgan 1991). The extinct vampire bat, *Desmodus archaeadaptus*, is presently known only from early Irvingtonian sites in Florida (Morgan et al. 1988, Morgan 1991). Bats are generally absent or very rare in faunas that sample fluvial or estuarine depositional environments such as Leisey. The presence of several teeth and limb bones of a small species of the tree bat *Lasiurus* from the De Soto Shell Pit is most unusual because this site appears to have formed in a shallow marine environment.

Comparative Analysis of Florida Irvingtonian Small Mammal Faunas

The composition of the microvertebrate fauna from Leisey is fundamentally different from that of Inglis 1A, Haile 16A, and Coleman 2A. The latter three faunas were collected from fissure or cave deposits in the northern half of the Florida peninsula. They are dominated by terrestrial vertebrates and to a much lesser extent freshwater taxa, but none of the three sites has the estuarine/marine component found at Leisey. Minimal transport was involved in the deposition of the three north Florida Irvingtonian sites, and as a result, small, delicate bones were preserved in large numbers. Insectivores, bats, and small rodents are very common in Inglis 1A, Haile 16A, and Coleman 2A, whereas members of these three groups are either absent or rare at Leisey. The abundance of cave-dwelling

Table 8. Occurrence of Insectivora, Lagomorpha, and Rodentia in selected Florida Irvingtonian faunas. "X" indicates a definite identification, "-" an absence, and "?" a possible identification. "T" indicates that the record represents the type locality for this species.

	earliest Irvingtonian		late early Irvingtonian				middle Irvingtonian	late Irvingtonian
	Inglis 1A	De Soto Shell Pit	Haile 16A	Leisey Shell Pit	Payne Creek Mine	Haile 21A	McLeod Limerock Mine ¹	Coleman 2A
	<i>Blarina</i> cf. <i>B. carolinensis</i>	X	X	X	X	X	-	-
<i>Cryptotis</i> cf. <i>C. parva</i>	X	-	X	-	-	-	-	X
<i>Scalopus aquaticus</i>	X	-	X	-	X	-	-	X
<i>Lepus</i> cf. <i>L. townsendii</i>	-	-	-	X	-	-	-	-
<i>Lepus</i> sp.	X ²	-	-	-	X	-	X	X ²
<i>Sylvilagus webbi</i>	T	X	X	-	-	-	-	-
<i>Sylvilagus palustris</i>	-	-	-	-	X	-	-	-
<i>Sylvilagus floridanus</i>	-	-	-	X	X	X	-	X
<i>Sylvilagus</i> sp.	-	-	-	-	-	-	X	-
<i>Glaucomys</i> sp.	X ³	-	-	-	-	-	-	X
<i>Sciurus carolinensis</i>	X	X	X	-	-	-	-	X
<i>Castoroides leiseyorum</i>	-	-	-	T	-	-	-	-
<i>Geomys propinetus</i>	T	X	X	-	-	-	-	-
<i>Geomys pinetis</i>	-	-	-	X	X	X	-	X
<i>Thomomys orientalis</i>	-	-	-	-	-	-	-	X
<i>Zapus</i> sp.	-	-	X	-	-	-	-	-
<i>Erethizon kleini</i>	T	-	-	-	-	-	-	-
<i>Erethizon dorsatum</i>	-	-	X	X	-	X	-	X
<i>Nechoerus</i> sp.	-	?	-	X	-	-	-	-

<i>Hydrochaeris holmesi</i>	X	-	-	-	-	-	-	X
<i>Neotoma</i> sp.	X	-	-	-	-	-	-	-
<i>Ochrotomys nuttalli</i>	-	-	-	-	-	-	-	X
<i>Peromyscus</i> small sp. ⁴	X	-	X	-	-	-	-	X
<i>Peromyscus</i> large sp. ⁵	-	X	-	-	X	X	-	-
<i>Podomys</i> sp. ⁶	-	-	X	X	-	-	-	-
<i>Podomys floridanus</i>	-	-	-	-	-	-	-	X
<i>Reithrodontomys</i> sp.	X	X	X	-	-	-	-	-
<i>Reithrodontomys humulis</i>	-	-	-	-	-	-	-	X
<i>Sigmodon curtisi</i>	X	X	-	-	-	-	-	-
<i>Sigmodon minor</i>	-	X	-	-	-	-	-	-
<i>Sigmodon libitinus</i>	-	-	T	X	X	X	-	-
<i>Sigmodon bakeri</i>	-	-	X	-	-	-	X	T
<i>Atopomys salvelinus</i>	-	X	-	-	-	-	-	-
<i>Neofiber leonardi</i>	-	-	-	-	-	-	X	-
<i>Neofiber alleni</i>	-	-	-	-	-	-	-	X
<i>Ondatra idahoensis</i>	X	X	-	-	-	-	-	-
<i>Ondatra annectens</i>	-	-	-	X	X	-	-	-
<i>Pedomys new</i> sp.	-	-	X	X	X	-	-	-
<i>Pitymys aratai</i>	-	-	-	-	-	-	-	T
<i>Synaptomys</i> sp.	-	-	X	X	-	-	-	-

¹The small mammal fauna from McLeod was not examined in detail, and therefore is almost certainly incomplete.

²The *Lepus* from Coleman 2A and Inglis 1A were originally referred to *Lepus alleni* on the basis of femora (Martin 1974; Webb and Wilkins 1984); however, the *Lepus* mandibles from Inglis are not *L. alleni* and the Coleman sample lacks the diagnostic p3.

³The Inglis 1A *Glaucomyia* is a new species currently being described by A. E. Pratt.

⁴*Peromyscus* small sp. probably includes several species in the size range of *P. gossypinus* and *P. polionotus*.

⁵*Peromyscus* large sp. is a large species in the size range of *P. cumberlandensis*.

⁶*Podomys* sp. appears to be a new species that is larger than *P. floridanus*.

bats in these three sites, in particular a species of *Myotis*, indicates deposition in a cave environment.

Morgan and Hulbert (this volume) review the Irvingtonian vertebrate faunas presently known from Florida. Their paper and the references cited therein should be consulted for more complete data on the location, geology, and vertebrate faunas from these sites. Table 8 shows the occurrence and chronological distribution of the 40 species of Insectivora, Lagomorpha, and Rodentia currently known from eight Florida Irvingtonian sites. This table does not include all Irvingtonian faunas from Florida, only those with five or more species of small mammals. Several other Florida Irvingtonian sites containing diagnostic specimens of rodents (e.g. Apollo Beach) are briefly discussed at the end of this section. The Marsupialia and Chiroptera are not included in Table 8 because these two orders are absent at Leisey. The following are synopses of the small mammal faunas from the Florida Irvingtonian sites listed in Table 8. Each of these faunas is compared and contrasted with Leisey.

Inglis 1A, Citrus County.--Inglis 1A has the richest small mammal fauna of any Florida Irvingtonian site, although many of the taxa have not been thoroughly studied. A preliminary list of the mammals from Inglis 1A has been published (Webb 1974; Webb and Wilkins 1984). Morgan (1991) briefly discussed the rich chiropteran fauna from Inglis 1A. The Inglis small mammals include 24 species: three species of insectivores, seven bats, three lagomorphs, and eleven rodents. Leisey shares eight of its twelve genera of small mammals with Inglis 1A. Among the four Leisey genera absent from Inglis 1A, *Castoroides*, *Pedomys*, and *Synaptomys* are biochronologically significant since their earliest records appear to be in late early Irvingtonian sites such as Leisey. Leisey and Inglis share at most two species of small mammals, and even these are questionable. Five taxa of small mammals from these two sites are congeneric but differ at the species level (Inglis species first/Leisey species second): *Geomys propineticus*/*G. pineticus*; *Erethizon kleinii*/*E. dorsatum*; *Sigmodon curtisi*/*S. libitinus*; *Ondatra idahoensis*/*O. annectens*; and *Sylvilagus webbi*/*S. floridanus*. Inglis 1A shares *G. propineticus* and *S. webbi* with several Florida late Blancan faunas. *O. idahoensis* is found in latest Blancan and earliest Irvingtonian faunas in western North America. *S. curtisi* appears to be restricted to the earliest Irvingtonian. The best estimate for the age of the Inglis 1A LF based on both small and large mammals is earliest Irvingtonian (latest Pliocene) between 1.9 and 1.6 Ma.

De Soto Shell Pit, De Soto County.--The De Soto Shell Pit has a limited, although quite interesting, small mammal fauna. This site actually possessed an abundance of microvertebrates, but the pit filled with water before UF crews were able to conduct extensive screenwashing operations there. The De Soto Shell Pit LF includes 12 species of small mammals: one species of insectivore, one bat, one rabbit, and nine rodents. The De Soto and Leisey 3A sites apparently formed

under similar depositional conditions. Both have large samples of aquatic vertebrates, including freshwater and estuarine taxa, along with a less diverse fauna of terrestrial microvertebrates. The De Soto Shell Pit LF has a number of genera but very few species of small mammals in common with Leisey. De Soto and Inglis 1A share four species of biochronologically diagnostic small mammals: *Geomys propinetus*, *Sigmodon curtisi*, *Ondatra idahoensis*, and *Sylvilagus webbi*. None of these species occur at Leisey. *O. idahoensis* and *S. curtisi* appear to be restricted to earliest Irvingtonian faunas in Florida. De Soto is the only Florida locality in which the diminutive cotton rat, *S. minor*, occurs. This species is otherwise known only from faunas in the western United States. *S. minor* has been synonymized with the Blancan *S. medius* by several authors (e.g. Martin 1986). The two forms differ in size, as this lineage of *Sigmodon* underwent a dwarfing event sometime in the late Pliocene. The *S. minor* teeth from De Soto are noticeably smaller than comparable Florida *S. medius* teeth, and therefore we have chosen to tentatively regard them as separate species. The presence of the primitive arvicoline *Atopomys salvelinus* and a large undescribed *Peromyscus* (or possibly *Podomys*) suggests that the De Soto Shell Pit LF may be slightly younger than Inglis 1A, although it is still earliest Irvingtonian in age.

Haile 16A, Alachua County.—Many of the small mammals from Haile 16A have been described in taxonomic studies on selected species, but Morgan and Hulbert (this volume) provide the only faunal list of mammals from this site. The small mammal fauna from Haile 16A consists of 17 species: three insectivores, two bats, one rabbit, and eleven rodents. Leisey and Haile 16A have eight genera and six species in common. *Castoroides*, *Nechoerus*, *Ondatra*, and *Lepus* are present at Leisey, but absent from Haile 16A. Species shared by these two faunas include: *Blarina* cf. *B. carolinensis*, *Erethizon dorsatum*, *Sigmodon libitinus*, and undescribed species of *Podomys*, *Pedomys*, and *Synaptomys*. The two genera in which the species from Haile 16A and Leisey differ at the species level are *Geomys* and *Sylvilagus*. The records of *G. propinetus* and *S. webbi* from Haile 16A are the youngest for these species, which otherwise are found in late Pliocene (late Blancan and earliest Irvingtonian) faunas in Florida. The occurrence of the larger and more evolutionarily advanced species *G. pinetis* at Leisey indicates this site is probably slightly younger than Haile 16A. Winkler and Grady (1990) reported *Atopomys salvelinus* from Haile 16A, a species supposedly characteristic of middle Irvingtonian faunas. Although its biochronological significance is unknown, the only known Florida occurrence of the zapodid rodent *Zapus* is from Haile 16A. The Haile 16A *Zapus* represents the southernmost known sample of this genus. It differs in several dental features from the extant eastern species, *Z. hudsonius*. Overall, Haile 16A and Leisey have very similar small mammal faunas suggesting that the two sites are close in age, with Haile 16A probably slightly older.

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. The small mammal fauna suggests that an early Irvingtonian age is more likely. Four species of mammals from Haile 16A indicate that this site is older than Leisey. Three of these are Blancan holdovers in which this site represents their youngest known occurrence. However, Haile 16A has more species in common with Leisey and other late early Irvingtonian sites. The faunal evidence suggests that Haile 16A falls in the middle third of the early Irvingtonian (between 1.6 and 1.3 Ma), younger Inglis 1A and De Soto Shell Pit and slightly older than Leisey Shell Pit.

Payne Creek Mine, Polk County.--The small mammals from the Payne Creek Mine LF have not been mentioned previously in the literature. The ten species of small mammals identified from this site are listed in Table 8, including two insectivores, three rabbits, and five rodents. Among these taxa, all but *Scalopus aquaticus* and *Sylvilagus palustris* are shared with Leisey. Furthermore, at least five of the species in common between these two faunas are good biochronologic indicators. Among these five species, *Sigmodon libitinus*, *Ondatra annectens*, and an undescribed species of *Pedomys* are limited to the late early Irvingtonian in Florida. The presence of *Sylvilagus floridanus* and *Geomys pinetis* at Payne Creek and Leisey, as well as *S. palustris* from Payne Creek, represent the earliest records of these species in Florida. Comparisons of both small and large mammals suggest that the Payne Creek Mine LF is closest in age to Leisey among currently known Florida Irvingtonian faunas.

Haile 21A, Alachua County.--Haile 21A has a rather limited small mammal fauna composed of seven species, including two bats, a rabbit, and four rodents. This site shares three species with Leisey and Payne Creek Mine, *Sylvilagus floridanus*, *Geomys pinetis*, and *Sigmodon libitinus*. The first two of these are living species that appear during the latter half of the early Irvingtonian, while *S. libitinus* is restricted to the Florida early Irvingtonian.

McLeod Limerock Mine, Levy County.--Several taxa of small mammals are known from the McLeod LF even though this site was discovered in 1941 before the advent of extensive screenwashing. McLeod is the only major Florida Irvingtonian site not housed in the UF vertebrate paleontology collection, and as a consequence we did not have the opportunity to examine the small mammals from this fauna. We are grateful to Richard Hulbert and Robert Martin for providing preliminary identifications of several taxa of McLeod rodents. Only four species from McLeod are listed in Table 8, two rabbits and two rodents, although we strongly suspect that other taxa of small mammals are present in this fauna but have not yet been identified. The only small mammal previously reported from McLeod is the extinct round-tailed muskrat *Neofiber leonardi* (Frazier 1977), representing the sole record of this species in Florida. Other localities in western

North America where *N. leonardi* is known to occur, including Rezabek (type locality) and Kanopolis in Kansas and Slaton in Texas, are generally considered late Irvingtonian. Martin (pers. comm.) has tentatively identified *Sigmodon bakeri* from McLeod. This Florida endemic is known from the Coleman 2A LF, as well as several early Rancholabrean sites. Although both diagnostic small mammals identified from McLeod seem to suggest a late Irvingtonian age, this site is clearly older than Coleman 2A. Several large mammals from this site, including *Smilodon gracilis* (see Berta 1987) and *Tapirus haysii* (see Hulbert this volume), are more typical of middle Irvingtonian faunas. McLeod is probably late middle Irvingtonian in age (0.7-0.6 Ma), although an early late Irvingtonian age is also possible.

Coleman 2A, Sumter County.--The most thoroughly studied small mammal fauna from the Irvingtonian of Florida is Coleman 2A (Martin 1974). The small mammals from Coleman 2A consist of 23 species, including three insectivores, three bats, two lagomorphs, fourteen rodents, and the opossum *Didelphis virginiana* (Martin 1974). Among the twelve genera of small mammals recorded from the Leisey Shell Pit LF, only *Castoroides*, *Ondatra*, and *Synaptomys* are absent from Coleman 2A (Table 8). Of the nine genera shared by Leisey and Coleman, at least four appear to differ at the species level, further substantiating the disparity in age between these two sites indicated by the large mammals (Morgan and Hulbert this volume). *Sigmodon libitinus* occurs at Leisey, while the species, *S. bakeri* is found at Coleman 2A (Martin 1974, 1979). Leisey has an undescribed species of *Pedomys*, while *Pitymys aratai* is known only from Coleman 2A. Measurements of *Blarina* from Leisey and Coleman indicate that specimens from the latter site are somewhat larger, but the systematic and/or biochronologic significance of this difference is unknown. Coleman 2A represents the earliest fossil record of five species of small mammals otherwise restricted to the Rancholabrean and Recent, including *Didelphis virginiana*, *Neofiber alleni*, *Ochrotomys nuttalli*, *Podomys floridanus*, and *Reithrodontomys humulis*. The presence of the bear *Arctodus pristinus* and the wolf *Canis armbrusteri* at Coleman 2A substantiate an Irvingtonian age, as does the absence of *Bison*. The occurrence of *S. bakeri* in several early Rancholabrean faunas and the appearance of several extant species of small mammals strongly suggests that Coleman 2A is latest Irvingtonian in age probably between 0.4 and 0.3 Ma (Martin 1974).

Other Florida Irvingtonian Sites.--Several species of rodents are known from other Florida Irvingtonian faunas, in addition to the eight sites listed in Table 8 and discussed above. *Erethizon dorsatum* (see Frazier 1981) and *Nechoerus* (see Ahearn 1981) have been reported from Apollo Beach in Hillsborough County. The extinct porcupine *E. kleini* was recorded from the Merritt Island LF in Brevard County of probable early Irvingtonian age (Frazier 1981). Other previously unpublished records of Irvingtonian rodents from Florida include *Castoroides* from

Apollo Beach and the Crystal River Power Plant, *Ondatra annectens* from Pool Branch and *Sigmodon libitinus* from the Shell Materials Pit.

Biochronology of Florida Irvingtonian Small Mammals

Comparisons of the Insectivora, Lagomorpha, and Rodentia from the eight most diverse Florida Irvingtonian sites (see Table 8) reveal an important biochronologic sequence of faunas that generally reflects the ages indicated by the large mammals (see discussion in Morgan and Hulbert this volume). Certain lineages of rodents and rabbits (e.g. *Geomys*, *Sigmodon*, *Ondatra*, *Pedomys*, *Sylvilagus*) are useful in providing a subdivision of the Florida Irvingtonian. Figure 7 shows the known biochronologic ranges of 31 species of lagomorphs and rodents in the late Pliocene and Pleistocene of Florida. Small mammals restricted to the Blancan or Rancholabrean are included in Figure 7, although species from these two NALMA are not discussed in detail. The following are biochronological characterizations of the small mammal faunas from the five Irvingtonian subdivisions recognized here. A well documented biochronological framework such as that proposed here and by Morgan and Hulbert (this volume) is of obvious utility in a state where many sites occur in karst-derived deposits that are not amenable to more standard geochronologic methods such as lithostratigraphy, radioisotopic dating, and paleomagnetic stratigraphy.

Earliest Irvingtonian (1.9 to 1.6 Ma). Two Florida earliest Irvingtonian sites contain small mammal faunas, Inglis 1A and De Soto Shell Pit. The Forsberg Shell Pit in Charlotte County (Morgan and Hulbert this volume) appears to be of this same age, but so far has produced only a limited fauna of larger mammals. Four species of rodents are restricted to earliest Irvingtonian faunas in Florida: *Erethizon kleini*, *Sigmodon curtisi*, *S. minor*, and *Ondatra idahoensis*. However, both *S. minor* and *O. idahoensis* occur in late Blancan faunas in the western United States. Two other species found in Inglis 1A and De Soto Shell Pit, *Sylvilagus webbi* and *Geomys propineticus*, also occur in Florida late Blancan faunas, as well as the early Irvingtonian Haile 16A LF. The record of *Atopomys salvelinus* from the De Soto Shell Pit represents the earliest occurrence of this genus. Notable absences from Florida earliest Irvingtonian faunas are *Castoroides*, *Pedomys*, and *Synaptomys*, all of which appear during the late early Irvingtonian.

Late early Irvingtonian (1.6 to 1.0 Ma). Florida sites of late early Irvingtonian age possessing diagnostic small mammal faunas are Haile 16A, Leisey Shell Pit, Payne Creek Mine, and Haile 21A. Correlative faunas with few or no species of small mammals, but which have diagnostic taxa of larger mammals, include Apollo Beach, Crystal River Power Plant, Pool Branch, Punta

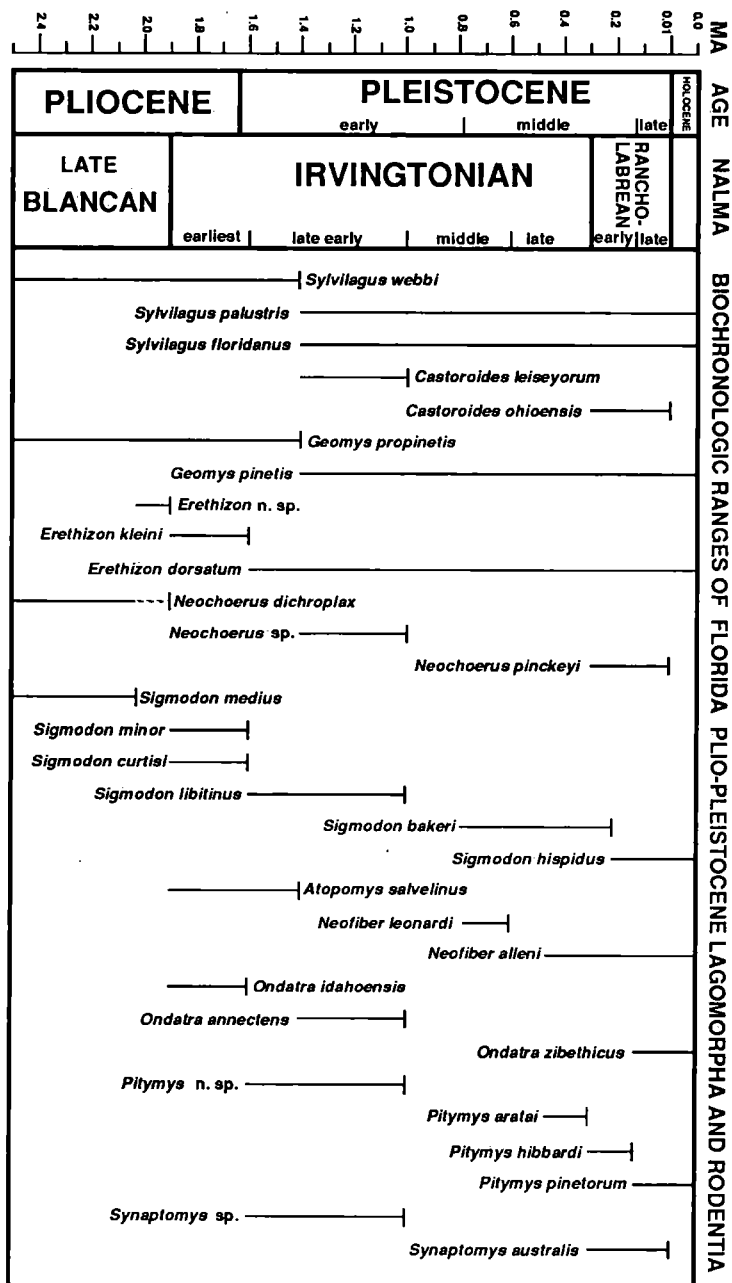


Figure 7. Biochronologic ranges of selected Rodentia and Lagomorpha from the late Pliocene and Pleistocene of Florida. *Pitymys* n. sp. is the same species discussed in the text as *Pedomys* sp.

Gorda, and Rigby Shell Pit (Morgan and Hulbert this volume). Six species of rodents are restricted to late early Irvingtonian faunas in Florida: *Castoroides leiseyorum*, *Zapus* sp., *Sigmodon libitinus*, *Ondatra annectens*, and undescribed species of *Pedomys* and *Synaptomys*. Because *Castoroides leiseyorum* is currently known only from the Leisey Shell Pit, its biochronologic range is unknown. Records of *Castoroides* from Apollo Beach and the Crystal River Power Plant likely pertain to this species. *S. libitinus* is a Florida endemic, while *O. annectens* occurs in both late early and middle Irvingtonian faunas in western North America. Florida late early Irvingtonian faunas are further characterized by the first appearance of two living species of lagomorphs, *Sylvilagus floridanus* and *S. palustris*, and two extant rodents, *Geomys pinetis* and *Erethizon dorsatum*. Haile 16A appears to be slightly older than other Florida late early Irvingtonian faunas based on the presence of *Geomys propineticus* and *Sylvilagus webbi*. Haile 16A probably dates to the early half of the late early Irvingtonian (1.6 to 1.3 Ma), while Leisey Shell Pit, Payne Creek Mine, and Haile 21A fall in the latter half (1.3 to 1.0 Ma).

Middle Irvingtonian (1.0-0.6 Ma). Vertebrate faunas of middle Irvingtonian age are represented in Florida solely by the poorly known McLeod Limerock Mine LF in Levy County. Only two species of small mammals from McLeod are good biochronological indicators, *Neofiber leonardi* and *Sigmodon bakeri*. *N. leonardi* is not known from other Florida Irvingtonian faunas (Frazier 1977), but occurs primarily in late Irvingtonian faunas elsewhere in North America. *S. bakeri* is a Florida endemic previously reported from the late Irvingtonian Coleman 2A LF, as well as several early RanchoLabrean sites. Although the two most diagnostic species of small mammals so far identified from McLeod are more typical of late Irvingtonian faunas, several large mammals from this site are indicative of a middle Irvingtonian age. The conflicting biochronological evidence from the small and large mammals suggests that McLeod probably falls either in the latter part of the middle Irvingtonian or the early part of the late Irvingtonian, between 0.7 and 0.5 Ma.

Late Irvingtonian (0.6-0.3 Ma). The late Irvingtonian in Florida is represented by the Coleman 2A LF, unless the McLeod LF belongs in the early portion of this interval, in which case the biochronological ranges of several large mammals would have to be redefined. The only species that appears to be restricted to the late Irvingtonian in Florida is the extinct vole, *Pitymys aratai*. *Sigmodon bakeri* was originally described from Coleman 2A, but has also been reported from the older McLeod LF and the younger early RanchoLabrean Haile 7A, Bradenton, and Williston 3A local faunas (Martin 1974; 1979). Coleman 2A represents the earliest fossil record for several species of small mammals otherwise restricted to the RanchoLabrean and Recent, including *Didelphis virginiana*, *Ochrotomys nuttalli*, *Podomys floridanus*, *Reithrodontomys humulis*, and *Neofiber*

alleni. The only Irvingtonian record for the pocket gopher *Thomomys orientalis* is from Coleman 2A (Wilkins 1985). This extinct species is otherwise restricted to a few Florida Rancholabrean faunas (Simpson 1928; Wilkins 1985). Based on the large number of living taxa, Martin (1974) suggested that Coleman 2A was latest Irvingtonian in age, probably between 0.4 and 0.3 Ma.

Comparison of Leisey With Other North American Irvingtonian Small Mammal Faunas

There are no radiometric dates in direct association with any Florida Plio-Pleistocene vertebrate localities and the Leisey Shell Pit is the only Florida Irvingtonian site with a known paleomagnetic signature (reversed-Matuyama Chron, see MacFadden this volume). The age of Leisey and other Florida Irvingtonian faunas must be determined primarily by biochronological comparisons with well-dated faunas from the western United States. However, the small mammals from Leisey are difficult to correlate with non-Florida Irvingtonian sites because of faunal provincialism (Lundelius et al 1987). The modern small mammals of Florida, particularly the rodents, consist mostly of species restricted to eastern North America, many of which are further limited to the southeastern United States. This regionalism was probably typical of the late Pliocene and Pleistocene as well, and thus it is not surprising that Florida Irvingtonian sites share few species with well known faunas of similar age from western North America.

In eastern North America, small mammal faunas representing the late Blancan and early Irvingtonian NALMA are currently known only from Florida. Several middle Irvingtonian (Irvingtonian II of Repenning 1987) small mammal faunas are recognized from the Appalachian region, including Cumberland Cave in Maryland, Hamilton Cave and Trout Cave in West Virginia, and Port Kennedy Cave in Pennsylvania (Kurtén and Anderson 1980; Repenning and Grady 1988). As previously noted by Guilday (1971), there are only a few species of small mammals in common between Florida and Appalachian Irvingtonian faunas. Guilday (1971:235) stated that, "The ecological disparity between those areas [i.e. Florida and the Appalachians] is, and presumably was during the past, too great to support a common fauna." These faunal distinctions appear to be related to the contrasting climatic and biogeographic histories of the two regions. Florida Irvingtonian faunas have a strong Neotropical influence, while those from the Appalachian region have a predominance of north temperate and boreal species. Despite these differences, we will concentrate on the taxonomic similarities between Florida Irvingtonian small mammal faunas and those from both the eastern and western United States.

Arvicoline rodents have been used extensively in Plio-Pleistocene biochronology in North America. Both Repenning (1980;1987) and L. D. Martin (1979) proposed biochronologies for the North American Pliocene and Pleistocene based solely on arvicoline rodents. Among the large number of Irvingtonian arvicoline faunas discussed by Repenning (1987), only the middle Irvingtonian (=Irvingtonian II) Cumberland Cave LF in Maryland is located in eastern North America. 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 (Martin 1974; Frazier 1977), which includes *Neofiber alleni* and *Pitymys aratai*, was not mentioned by Repenning (1987).

Arvicolines are principally temperate and boreal rodents, and accordingly 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 in the continental United States. Likewise, arvicoline rodents generally are uncommon in most Florida Pliocene and Pleistocene sites. Blancan faunas in the state lack arvicolines, whereas eight species of arvicolines occur in Florida Irvingtonian sites, including three from Leisey (Table 8).

Martin and Schultz (1985) named the Sappan subprovincial age, typified by the Sappa LF of Nebraska, for a number of early Irvingtonian vertebrate faunas from the Great Plains. The Sappan is equivalent to the early Irvingtonian of Lundelius et al. (1987) and Morgan and Hulbert (this volume) and the Irvingtonian I of Repenning (1987). Martin and Schultz characterized Sappan faunas by the co-occurrence of *Lepus*, *Allophaiomys*, *Mictomys kansasensis*, *Stegomastodon*, *Titanotylopus*, and the first North American appearance of *Mammuthus*. The genera *Mictomys*, *Stegomastodon*, and *Titanotylopus* are unknown from Florida; however, *Lepus* and *Mammuthus* are present at Leisey. Leisey also shares the muskrat *Ondatra annectens* with many of these Sappan faunas. In addition to the Sappa LF, Sappan faunas include: the Java LF in South Dakota, the Kentuck, Nash, and Wathena local faunas in Kansas, the Holloman LF in Oklahoma, and the Gilliland LF in Texas (Hibbard and Dalquest 1966; Martin and Schultz 1985; Lundelius et al. 1987).

Morgan and Hulbert (this volume) considered many of these same early Irvingtonian faunas to be close correlatives of Leisey based on their large mammal faunas, in particular, Gilliland and Holloman. Small mammals are rare in the Gilliland and Holloman local faunas, whereas most of the Sappan faunas from South Dakota, Nebraska, and Kansas have limited samples of large mammals. Radiometric dates are available for several of these sites. The Nash LF occurs between volcanic ash beds dated at 1.96 and 1.2 Ma (Eshelman and Hibbard 1981), while the Sappa LF occurs just beneath an ash dated at 1.2 Ma (Martin and Schultz 1985). The western Sappan faunas discussed above and the correlative faunas from Florida, including Leisey Shell Pit, Haile 16A, Payne Creek Mine, and Haile

21A among others, belong to the Pleistocene portion of the early Irvingtonian between 1.64 and 1.0 Ma. This is a rather long interval of time covering nearly two-thirds of a million years, thus allowing for a substantial range of ages among the included faunas.

Earliest Irvingtonian (latest Pliocene) faunas are distinctly older than the Leisey Shell Pit LF based on differences in both the small and large mammals. Two Florida faunas are earliest Irvingtonian in age, Inglis 1A and De Soto Shell Pit. Perhaps the most distinctive feature of these two faunas is the presence of Blancan holdovers, including the hyaenid *Chasmaporthetes ossifragus*, the mustelid *Trigonictis macrodon*, the antilocaprid *Capromeryx arizonensis*, and the dwarf Florida form of the ground sloth *Megalonyx leptostomus*, as well as *Geomys propinectis* and *Sylvilagus webbi* among small mammals. None of these species occur at Leisey. *Trigonictis*, *G. pinetis*, and *S. webbi* are also present in the Haile 16A LF, which is intermediate in age between the older Inglis and De Soto faunas and the younger Leisey fauna. *Mammuthus* is absent from earliest Irvingtonian faunas, as well as Haile 16A. Inglis and De Soto correlate most closely with the Curtis Ranch LF in Arizona, the Vallecito Creek LF in California, and the Wellsch Valley LF in Saskatchewan. Based on paleomagnetic polarity stratigraphy these three western earliest Irvingtonian faunas appear to fall either just before, within, or just after the Olduvai Normal Subchron of the Matuyama Chron (Lundelius et al. 1987). The range of ages for these faunas is between 1.9 and 1.64 Ma, from the Blancan/Irvingtonian boundary to the beginning of the Pleistocene.

Comparisons between Leisey and Irvingtonian sites from outside of Florida reveal certain similarities with middle Irvingtonian faunas (=Cudahyan of Lundelius et al. 1987 and Irvingtonian II of Repenning 1987). Typical western faunas of this age (1.0 to 0.6 Ma) include the Cudahy LF in Kansas, Conard Fissure LF in Arkansas, and Vera LF in Texas. The Cudahy and Vera faunas both occur below ashes radiometrically dated at 0.61 Ma (Lundelius et al. 1987). Several cave faunas from the Appalachian region have been regarded as middle Irvingtonian in age as well, the best known of which are Cumberland Cave, Port Kennedy Cave, Hamilton Cave, and Trout Cave (Kurtén and Anderson 1980; Repenning and Grady 1988). None of the Appalachian Irvingtonian sites have absolute dates and their relative ages have been determined by biochronological comparisons. Repenning and Grady restricted the age of Hamilton Cave to between 0.85 and 0.74 Ma based on its extensive arvicoline fauna. Leisey shares only one arvicoline with Hamilton Cave, the muskrat *Ondatra annectens*, a long-ranging species typical of both late early and middle Irvingtonian faunas (late Irvingtonian I and Irvingtonian II of Repenning 1987). The primitive arvicoline *Atopomys* is not known from Leisey but is found in Haile 16A and De Soto Shell Pit. Although *Atopomys* is restricted to middle Irvingtonian faunas according to Winkler and Grady (1990), both Florida faunas containing this genus are early Irvingtonian.

Leisey also shares several species of large mammals with Port Kennedy Cave, Cumberland Cave, and Hamilton Cave. Four large carnivores, including the cheetah-like cat *Miracinonyx inexpectatus*, the sabercat *Smilodon gracilis*, the tremarctine bear *Arctodus pristinus*, and the wolf *Canis armbrusteri*, as well as the ground sloth *Megalonyx wheatleyi*, occur at Leisey and in one or more of these three Appalachian middle Irvingtonian cave deposits (Guilday 1971; McDonald 1977; Kurtén and Anderson 1980; Van Valkenburgh et al. 1990).

On the basis of mammalian biochronology, the Leisey Shell Pit LF correlates most closely with the latter half of the early Irvingtonian between 1.3 and 1.0 Ma. Faunal criteria strongly suggest that Leisey is younger than earliest Irvingtonian faunas such as Inglis 1A and De Soto Shell Pit (i.e. younger than about 1.6 Ma) and older than the late middle Irvingtonian McLeod Limerock Mine LF (i.e. older than 0.7 Ma). Biochronological data further restrict the age of Leisey to the latter half of the early Irvingtonian. Geochronological data rule out an early middle Irvingtonian age (between about 1.0 and 0.78 Ma, see other papers in this volume by Morgan and Hulbert; Jones et al; and MacFadden). The similarity of Leisey to certain middle Irvingtonian vertebrate faunas suggests that it falls late in the early Irvingtonian interval, and accordingly may be no more than several hundred thousand years older than Cumberland Cave, Hamilton Cave, and Port Kennedy.

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