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**THE BROOKSVILLE 2 LOCAL FAUNA
(ARIKAREEAN, LATEST OLIGOCENE):
HERNANDO COUNTY, FLORIDA**

F. Glynn Hayes

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THE BROOKSVILLE 2 LOCAL FAUNA (ARIKAREEAN, LATEST OLIGOCENE): HERNANDO COUNTY, FLORIDA

F. Glynn Hayes¹

ABSTRACT

Vertebrate fossils from fissure fill deposits in the Suwannee Limestone located near the town of Brooksville, Hernando County, Florida, represent at least 27 mammalian species, constituting the Brooksville 2 Local Fauna. Taxa from the Brooksville 2 Local Fauna that include first occurrences in Florida are *Agnotocastor*, *Megalagus*, *Palaeogale*, *Enhydrocyon*, and an Entoptychine rodent. Described in detail are two insectivores (*Centetodon*, *Parvericius*), the lagomorph (*Megalagus abaconis* n. sp.), the castorid (*Agnotocastor* sp.), and all carnivores (*Palaeogale*, two new musteloids: *Acheronictis webbi* n. gen. et sp., *Arikarictis chapini* n. gen. et sp., and three canids: *Enhydrocyon*, *Osbornodon wangi* n. sp., *Phlaocyon taylori* n. sp.). Biochronologic correlation indicates the age of the fauna is within the undefined biochronologic interval of the "medial" Arikareean NALMA (latest Oligocene). The Brooksville 2 Local Fauna is correlative with the Cow House Slough Local Fauna and SB-1A Local Fauna.

RESUMEN

La fauna local Brooksville 2 está constituida por fósiles de vertebrados, representando al menos 27 especies de maníferos, que fueron encontrados en fisuras de rocas sedimentarias de Suwannee cerca del pueblo de Brooksville en el condado de Hernando de la Florida. La fauna local de Brooksville 2 incluye taxones representados por primera vez para *Agnotocastor*, *Megalagus*, *Palaeogale*, *Enhydrocyon* y un roedor Entoptychino. Se describen en detalle dos insectívoros (*Centetodon*, *Parvericius*), el lagomorfo (*Megalagus abaconis* n. sp.), el castorido (*Agnotocastor* sp.), y los carnívoros (*Palaeogale*, dos nuevos musteloideos: *Acheronictis webbi* n. gen. et sp., *Arikarictis chapini* n. gen. et sp., y tres cánidos: *Enhydrocyon*, *Osbornodon wangi* n. sp. y *Phlaocyon taylori* n. sp.). La correlación biocronológica indica que la edad de esta fauna está dentro del intervalo biocronológico indefinido del Arikareano "medio" NALMA (Oligoceno más tardío). La fauna local Brooksville 2 es correlativa con la fauna local de Cow House Slough y con la fauna local SB-1A.

TABLE OF CONTENTS

Introduction	2
Acknowledgments	4
Geography and Geology	4
Brooksville 2 Local Fauna	6
Taphonomy	8
Systematic Paleontology	10
Insectivora	
<i>Centetodon</i>	10
<i>Parvericius</i>	12
Rodentia	
<i>Agnotocastor</i> sp.	14
Lagomorpha	
<i>Megalagus abaconis</i> n. sp.	18
Carnivora	
<i>Palaeogale minuta</i>	23
<i>Acheronictis webbi</i> n. gen. et sp.	26
<i>Arikarictis chapini</i> n. gen. et sp.	30
<i>Enhydrocyon</i> cf. <i>pahinsintewakpa</i>	31
<i>Osbornodon wangi</i> n. sp.	32
<i>Phlaocyon taylori</i> n. sp.	34
Age and Correlation	37
Summary	42
Literature Cited	44

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INTRODUCTION

The Arikareean North American Land Mammal "Age" (NALMA) spans the late Oligocene-early Miocene boundary. In Florida this interval has been poorly represented until recently. In Simpson's (1930) early summary of Miocene land mammals from Florida, he described the first Arikareean fauna from Florida, Franklin Phosphate Pit No. 2 (FPP2). Two years later, Simpson (1932) described the famous Hemingfordian Thomas Farm locality and reviewed the five faunas described in 1930. He suggested that FPP2, on a "necessarily vague and personal impression might be rather older" than the other faunas (Simpson, 1932:15). This proved correct, because FPP2 is still considered Arikareean in age, whereas the other four localities are presently assigned to the Hemingfordian or even the Barstovian Land Mammal "Ages."

The second Arikareean fauna came from Brooksville, Florida, and was briefly described by Patton (1967), based on four specimens that were "more advanced than corresponding Late Oligocene forms, yet more primitive than those of the Middle Miocene."

During the 1970s two more extensive Arikareean faunas were reported from Florida: the SB-1A Local Fauna near Live Oak (Frailey, 1978), and the Buda Local Fauna from Alachua County (Frailey, 1979). Both faunas included significant additions to the record of Florida diversity, and Frailey was able to identify, for the first time, Arikareean taxa from the Great Plains in Florida, e.g., *Nanotragulus loomisi*. In addition, a new amphicyonid from the Buda Local Fauna, *Daphoenodon notianastes*, was recognized in the Brooksville Fauna of Patton (1967) and in the FPP2 Local Fauna. The presence of this carnivore, known only from Arikareean sites in the midcontinent, strengthens the correlation of these faunas with each other and the Arikareean NALMA.

After the discovery of Buda and SB-1A, MacFadden (1980) described a small sample from a roadcut in Marion County, Florida. This site included an Arikareean oreodont embedded in marine limestone and a few other isolated specimens that were found in clastic sediments just above the oreodont. Together these samples make up the Martin Anthony Local Fauna, one of the few Florida assemblages that has some lithostratigraphic control rather than occurring in a karst feature.

The late 1980s brought the discovery of two more Arikareean faunas: the White Springs Local Fauna and the Cow House Slough Local Fauna. The White Springs Fauna is unique in that it is mainly comprised of several articulated oreodont skeletons preserved in a nearshore

marine facies. Morgan (1989) summarized the oreodonts and other isolated taxa discovered with them, assigning a late Arikareean age by comparison with Great Plains' species. In the same paper, Morgan also first mentioned the Arikareean Cow House Slough Local Fauna from Hillsborough County, Florida. Although Morgan (1993) later discussed Cow House Slough again in more detail in his summary of mammalian Neogene biochronology of Florida, this diverse fauna still remains undescribed.

Another important fauna that illuminates the Arikareean of the Gulf Coastal Plain is the Toledo Bend Local Fauna of east Texas (Albright, 1991, 1994, 1996). This fauna is diverse (42 vertebrates, including 27 mammal species). It contains some of the same taxa as Buda, FPP2, and Cow House Slough.

In his ongoing study of the Toledo Bend Local Fauna, Albright (1998) recently discussed the Arikareean faunas in Texas and Florida in relation to the more developed midcontinental sequences of Arikareean age. In this paper, Albright reviewed the eight Arikareean Florida faunas and mentioned that a new rich fauna of Arikareean age from Florida was currently under study by this author.

The Brooksville 2 Local Fauna represents the ninth addition to the Arikareean faunas of Florida. It was uncovered near the town of Brooksville by amateur fossil hunters of the Florida Paleontological Society in 1994. Because of their geographic proximity to the town of Brooksville, this series of samples is called the Brooksville 2 Local Fauna, while the original material described by Patton (1967) becomes the Brooksville 1 LF.

The Brooksville 2 Local Fauna is, to date, the most speciose of the Arikareean faunas found in Florida. Its 27 mammalian species rivals the Toledo Bend LF. Brooksville 2 LF contains more microvertebrate taxa, whereas Toledo Bend LF has a predominance of larger ungulates. The new fossils from Brooksville provide a basis for broader comparisons between the Gulf Coastal Plain and the classic samples of Arikareean age from both the midcontinent and the John Day Basin of Oregon (see Tedford et al., 1987, 1996).

This report on the Brooksville 2 Local Fauna provides: a synopsis of the total vertebrate fauna; a discussion of the taphonomy of the fauna; a detailed systematic review of the insectivores, castorids, lagomorphs, and carnivores; and a section on the age and correlation of the Brooksville 2 LF with discussion of correlations within the Arikareean NALMA. Some other components of the fauna are to be reported on in further detail by collaborators in the future.

Identification of mammal taxa was based on jaws and teeth, which provided reliable characters for species

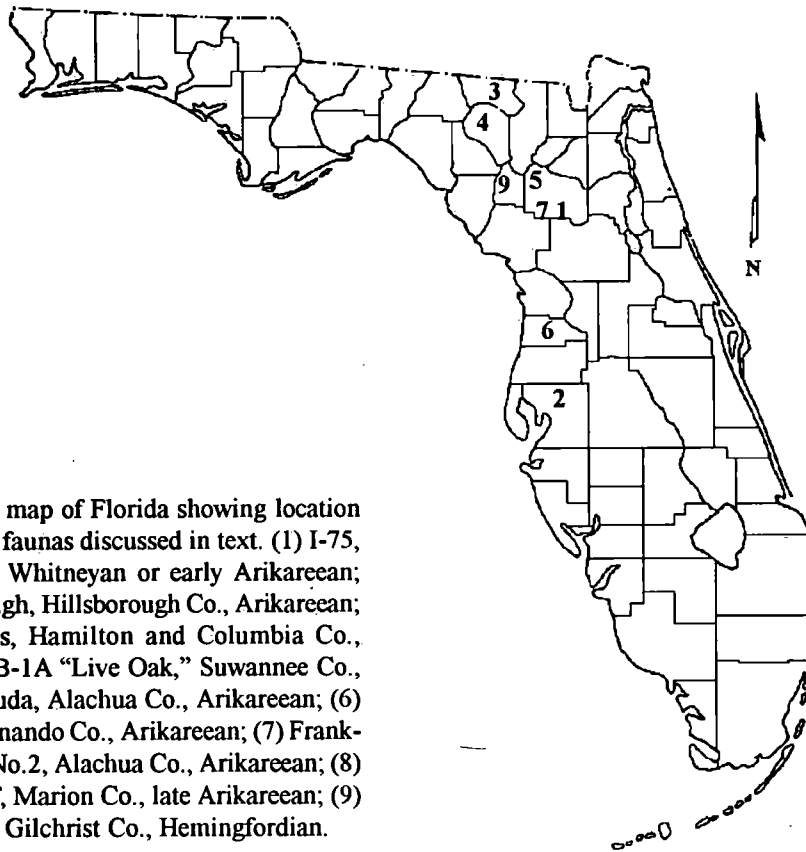


Figure 1. Outline map of Florida showing location of vertebrate local faunas discussed in text. (1) I-75, Alachua Co., late Whitneyan or early Arikareean; (2) Cowhouse Slough, Hillsborough Co., Arikareean; (3) White Springs, Hamilton and Columbia Co., Arikareean; (4) SB-1A "Live Oak," Suwannee Co., Arikareean; (5) Buda, Alachua Co., Arikareean; (6) Brooksville 1, Hernando Co., Arikareean; (7) Franklin Phosphate Pit No.2, Alachua Co., Arikareean; (8) Martin-Anthony F, Marion Co., late Arikareean; (9) Thomas Farm LF, Gilchrist Co., Hemingfordian.

designation. However, like most Florida Arikareean faunas, nearly all the fossils consisted of isolated teeth and disarticulated postcranials. These were sorted preliminarily according to size and general morphology. Comparisons were then made with other Arikareean faunas (using examples of complete or associated specimens representing the same or closely related taxa) in the collections of the Florida Museum, the American Museum, and the University of Nebraska State Museum. Musteloid material was compared at the University of Nebraska, where casts of relevant European material were available, and was carried out in Europe by M. Wolsan (written communication, 1998) using original material.

Where I have encountered new species, I have named them utilizing the most diagnostic isolated tooth as the holotype. Clearly the diagnosis of such species depends upon the sample, not only the holotype. I have made associations of isolated material on the following bases: (1) composite material is assembled on the basis of detailed comparison with more complete similar taxa from other faunas; (2) size and morphology of a fossil are consistent with derivation from only a single species; (3)

the material is unique; and (4) the composite material displays apparent differences relative to other taxa.

All the specimens comprising the Brooksville 2 Local Fauna are curated in the Collection of Fossil Vertebrates, housed in the Florida Museum of Natural History, Gainesville, Florida. The dental terminology used for castorids is after Stirton (1935) and Korth (1996). Terminology for lagomorphs follows that of Wood (1940) and Dawson (1958). Other dental terminology employs standard tribosphenic nomenclature (Van Valen, 1966, fig. 1). Measurements were taken using metric calipers or, for smaller specimens, a Gertner measuring microscope was used. All measurements are in millimeters unless otherwise stated. Measurement parameters and nomenclature follow standard guidelines in the major published reviews or monographs for each taxon. In tables and text, a lower case letter indicates lower teeth (p1-4), while an upper case letter indicates upper teeth (P1-4). Generic and species names that appear in quotation marks are taxa of questionable or no longer valid nomenclature retained for purposes of discussion.

Abbreviations used (others defined in figures, tables,

or text): ap, anterior to posterior measurement, length; alv, alveolus; ca., circa with reference to dates; F, Fauna; Fm, Formation; LF, Local Fauna; M, sample mean; m# or M#, molar, lower case for lower molar; N, sample number; OR, observed range of variation; p# or P#, premolar; tr, transverse measurement, width; tra, transverse measurement of anterior trigonid width in lower teeth; trp, transverse measurement of posterior talonid width in lower teeth; S, standard deviation; UBI, undefined biochronologic interval.

Institutional abbreviations used: AMNH, American Museum of Natural History, New York NY; CMNH, Carnegie Museum of Natural History, Pittsburgh PA; F:AM, Frick fossil mammal collection, housed in the American Museum; FMNH, Field Museum of Natural History, Chicago IL; FSP, Faculte des Sciences, Poitiers, France; LSUMG V, Louisiana State University Museum of Geosciences, Vertebrates; PU, Princeton University collection (now at Yale Peabody Museum of Natural History, New Haven CT); SDSM, South Dakota School of Mines and Technology, Rapid City; UF, University of Florida Collections, Florida Museum of Natural History, Gainesville; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington DC.

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GEOGRAPHY AND GEOLOGY

LOCATION.—The Brooksville 2 Local Fauna was collected from an abandoned quarry of the Florida

Rock Industries Limerock Mine located in the SW 1/4, Section 20, Township 21 S, Range 19 E, of the Brooksville NW quadrangle. This is approximately eight kilometers to the northeast of the town of Brooksville, Hernando County, Florida. The deserted quarry is located 30 meters east of Highway 491A and north of the intersection of Highway 491A and U.S. Highway 98.

Crews from the Florida Museum of Natural History identified and collected five fossil terrestrial vertebrate-bearing sites, labeled 1A through 1E (see Fig. 2, inset). These were either from *in situ* clastic fillings of karst features or from adjacent spoil piles. Sites 1A and 1E were small pockets of laminated clay and sand sediments filling solution cavities a meter below the present surface on the southeast wall of the quarry face. Site 1B was positioned on the quarry floor in a shallow depression that was seasonally filled with water. Site 1C was a spoil pile on the west side of a pond in the northern part of the quarry floor. Site 1D was the smallest of the sites, located at the north end of the excavation along the walls of an access road. It is uncertain if 1D was in place or disturbed by construction of the road.

All matrix was recovered from sites 1A, 1B, and 1E and screen-washed through three screen sizes to retrieve vertebrate fossils. Localities 1C and 1D were not screen-washed because the sediment was not in place and fossils were scarce relative to sediment volume. The weights of matrix screen-washed were: 1A, 23.78 kg; 1B, 410.31 kg; and 1E, 63.71 kg.

REGIONAL GEOLOGY.—The Brooksville 2 LF occurs in the Brooksville Ridge region, the largest of Florida's central or midpeninsular ridges formed during Pleistocene sea level fluctuations (White, 1970). The Brooksville Ridge stretches north-south about 110 miles, but is divided at the Dunnellon Gap by the westward flow of the Withlacoochee River. The southern end is marked by the Zephyrhills Gap and the Hillsborough River, and the northern end is defined by the High Springs Gap and the Santa Fe River. The Brooksville Ridge has the most irregular surface of Florida's central ridges, with elevations ranging from 23 to 66 meters over small distances. This is due to differential exposure and weathering of soluble carbonates and resistant siliciclastics. A structural subsurface high, affecting early Oligocene and older sediments, is coincident with the Brooksville Ridge. The high is either the result of a gentle tectonic flexure (the Ocala Arch, Vernon, 1951) or it is an erosional remnant of the Ocala and older formations (the Ocala Platform, Scott, 1992).

The abandoned quarry from which the Brooksville 2 LF was collected consists primarily of early Oligocene Suwannee Limestone (Yon and Hendry, 1972). The

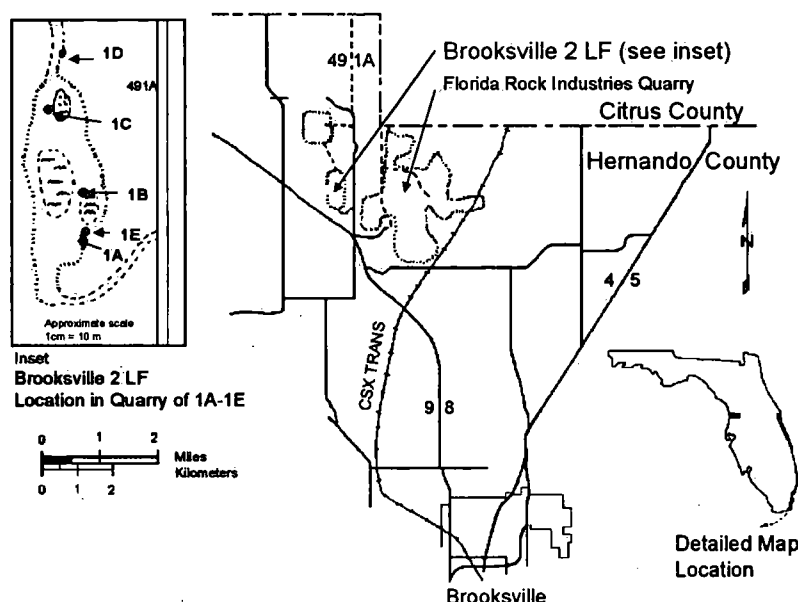


Figure 2. Location map of the Brooksville 2 Local Fauna.

Suwannee Limestone is a marine bioclastic calcarenite deposited in a shallow shelf environment. Parts of it are recrystallized and silicified. It has a tendency to become more arenaceous in its upper sections; the greater influx of siliciclastics reflects renewed uplift in the Appalachians during the Oligocene (Randazzo, 1997). The recrystallized sections (chert zones) are found in the subsurface highs of the Suwannee Limestone along the Brooksville Ridge. The top of the Suwannee Limestone forms an irregular surface in Hernando County resulting from uneven karst erosion during the low sea level stand of the Late Oligocene and Early Miocene (Yon and Hendry, 1972; Haq et al., 1987). This erosional interval may have formed the sinkholes that were then filled with the sediments that produced the Brooksville 2 LF.

To further constrain the age of the Brooksville 2 LF, limestone (4 samples) and invertebrate fossils (4 samples) were collected at or near the top of the Suwannee Limestone exposed in the Brooksville 2 LF quarry. These samples were then analyzed for strontium isotopic composition ($^{87}\text{Sr}/^{86}\text{Sr}$) in the Department of Geology at the University of Florida using standard techniques (Hodell et al., 1991). The measured isotopic ratios were converted to age estimates using the regression equations of Mead and Hodell (1995). The results gave an age of 35.5-33.3 Ma. This agrees with dates obtained for Suwannee Limestone elsewhere in Florida by Jones et al. (1993).

The sediments lying unconformably over the Suwannee Limestone are unfossiliferous clays and thin limestones. These have been assigned to the Tampa Fm or labeled as undifferentiated post-Oligocene (Yon and Hendry, 1972). Hunter (1970:20) suggested that there is no "tangible evidence of their proper stratigraphic position" even questioning whether they are necessarily of post-Oligocene age. Following Hunter, I propose to use the informal name "post-Suwannee" until such time as a reliable age and position can be established. Because of the uncertain placement of the post-Suwannee interval, these sediments cannot be used to help constrain the age of the Brooksville 2 LF.

The bottom of the quarry exposes the upper part of the Eocene Ocala Group (Crystal River Fm). The Eocene Ocala Group is composed of white to gray foraminiferal and molluscan packstones and grainstones deposited in a shallow to middle shelf environment (Randazzo, 1997). The Suwannee Limestone is separated from the Ocala by an unconformity of uncertain duration. Determination of the boundary between the Ocala and the Suwannee is difficult, as the limestone exposed in the quarry is rather homogeneous in overall lithology. In a section described by Hunter (1970) from the "Lansing quarry," now the operational Florida Rock Industries quarry, the Bumpnose Formation (included in the Crystal River Formation by Yon and Hendry, 1972) is listed as occurring several feet below the chert boulder zone of the

Suwannee Limestone. This chert zone is present in the abandoned quarry two or three meters above the quarry floor, and that is the lithological evidence that the Crystal River Formation is present.

More generally, in central Florida the three main lithological units described above are variable in their occurrence and superpositional relationships. In many areas the Suwannee Limestone is missing, either through erosion or nondeposition, and the Ocala Group directly underlies the post-Suwannee deposits. Along the crest of the Brooksville Ridge, and in many parts of central Florida, the Suwannee and post-Suwannee units are both missing, leaving only the Ocala Group at the surface.

THE BROOKSVILLE 2 LOCAL FAUNA

Table 1 is a preliminary list of the taxa comprising the Brooksville 2 Local Fauna. I am grateful to the colleagues acknowledged above for allowing me to cite their preliminary results, including the rodents, bats, reptiles, and amphibians. Presently, 46 species of vertebrates are listed in the fauna. Fishes are represented by two species of sharks (Chondrichthyes) and one of teleost (Osteichthyes). These are typical of the Oligocene marine Suwannee Limestone and are a reworked component of the fauna. Reptilia and Amphibia are very abundant in the fauna with at least three species of frogs (Anura), two salamanders (Urodela) including a siren, a small crocodile, a mud turtle (Kinosternidae), boid snakes (Serpentes), and three species of lizards (Squamata). Birds are rare in the fauna with only three postcranial bones representing the Galliformes. The mammalian taxa include a mouse-sized marsupial, two insectivores, three families of bats (Chiroptera), numerous rodents of seven families (Geomyidae, Sciuridae, Heteromyidae, Heliscomyidae, Florentiamyidae, Castoridae, Eomyidae), a rabbit (Lagomorpha), seven species of carnivores (Musteloidea, Canidae), one horse (Equidae), and three kinds of artiodactyls (Camelidae, Hypertragulidae, Merycoidodontidae). Figure 3 shows the relative abundances of mammal orders in the fauna, based on the minimum number of individuals for each taxon.

Over 60 teeth and a few jaws belong to the marsupial species. This sample is unusually large, as marsupials are generally rare in most localities (Korth, 1992). Analysis of the marsupial (Hayes and Wolff, in preparation) indicates that this material is a new species of *Herpetotherium*, possibly a descendant of "*Peratherium*" listed in the Whitneyan I-75 LF (Patton, 1969). Both these marsupials appear to be closely related to *H. merriami* (Stock and Furlong, 1922) from the John Day fauna of

TABLE 1.—Preliminary Brooksville 2 Local Fauna vertebrate faunal list.

<u>Chondrichthyes</u>	
	<i>Ginglymostoma</i> sp.
	<i>Carcharhinus</i> sp.
<u>Osteichthyes</u>	
	Teleostei: undet.
<u>Amphibia</u>	
	Anura: 3 Families present
	Urodela
	Sirenidae: n. gen. et sp.
	<i>Notothalmus</i> sp.
<u>Reptilia</u>	
	Crocodylia
	Chelonia
	Kinosternidae
	Serpentes
	Boidae
	<i>Calamagras</i> : 2-3 species, 1 n. sp.
	<i>Ogmophis</i> sp.
	<i>Geringophis</i> n. sp.
	Squamata
	Iguania
	Helodermatidae
	Anguidae
<u>Aves</u>	
	Galliformes: indet.
<u>Mammalia</u>	
	Marsupialia
	<i>Herpetotherium</i> n. sp.
	Insectivora
	<i>Parvericius montanus</i> *
	<i>Centetodon magnus</i> *
	Chiroptera
	Emballonuridae: n. sp.
	Mormoopidae: 2 n. sp.
	Vespertilionidae: n. sp.
	Rodentia
	Eomyidae
	Sciuridae
	Heliscomyidae
	Heteromyidae: 2 sp.
	Florentiamyidae
	Geomyidae-
	Entoptychinae: n. gen. et sp.
	Castoridae
	<i>Agnotocastor</i> sp.*
	Lagomorpha
	Leporidae
	<i>Megalagus abaconis</i> n. sp.*
	Carnivora
	<i>incertae sedis</i>
	<i>Palaeogale minutus</i> *
	Mustelida
	<i>Acheronictis webbi</i> n. gen. et sp.*
	<i>Arikarictis chapini</i> n. gen. et sp.*
	Canidae
	<i>Enhydrocyon</i> cf. <i>pahinsintewakpa</i> *
	<i>Osbornodon wangi</i> n. sp.*
	<i>Phlaocyon taylori</i> n. sp.*
	Perissodactyla
	Equidae
	<i>Miohippus</i> sp.
	Artiodactyla
	Camelidae
	<i>Nothokemas waldropi</i> .
	Hypertragulidae
	<i>Nanotragulus loomisi</i>
	Merycoidodontidae
	Phenacocoelinae: genus indet.

* Mammalian taxa described in detail in this paper.

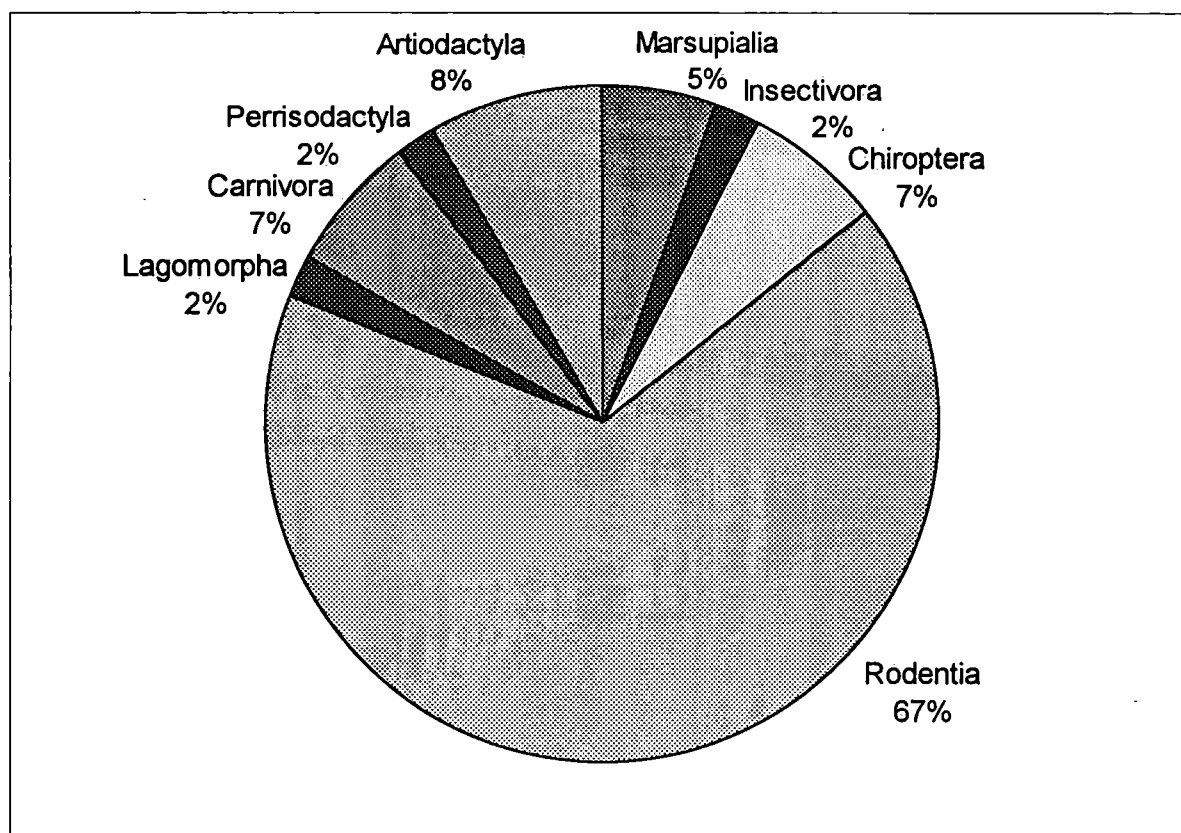


Figure 3. Relative abundances of mammal orders from the Brooksville 2 LF. Based on minimum number of individuals.

Oregon rather than to the Great Plains lineages of *Herpetotherium* (Green and Martin, 1976; Korth, 1994).

Two distinct genera, the immigrant hedgehogs *Parvericius* and *Centetodon*, represent insectivores. *Centetodon* is a common insectivore of the early Oligocene, but much rarer in later faunas (Lillegraven et al., 1981). Its terminal species is found in the Brooksville 2 LF and in the Buda LF.

The bats are some of the best-preserved material in the fauna with three families and four species present. Morgan's (pers. comm., 1996) preliminary work indicates that these are all undescribed species. The most common bat occurring in the fauna belongs to the Mormoopidae; the family at present has its northern limit in southernmost Arizona and Texas and ranges through Central America into southern Brazil (Nowak, 1999). The other two families are the Vespertilionidae and the Emballonuridae. Vespertilionids are found worldwide and have the widest ecological range of any bats, while the emballonurids, like the mormoopids, are restricted to the tropics and subtropics (Nowak, 1999).

Rodents are the most abundant vertebrates of the Brooksville 2 LF. Over seven families are present, with more than one species each in the Heteromyidae, Eomyidae, and Sciuridae. The geomyid belongs to the subfamily Entoptychinae that includes the genera *Pleurolicus*, *Gregorymys*, *Entoptychus*, and *Schizodontomys*. *Gregorymys* and *Entoptychus* are important as biostratigraphic indicators in the John Day beds in Oregon and the Great Plains (Rensberger, 1971, 1973, 1983; Tedford et al., 1987). The Brooksville entoptychine is closest to *Gregorymys* in morphology in that it is relatively low crowned with complex premolars, but it has several dental features in common with *Pleurolicus* and *Entoptychus* as well. Therefore, assignment to any known genus is doubtful. Castorids are represented in the fauna by *Agnotocastor* sp., which is fully described in the systematic section.

The carnivores are diverse and consist of a wide range of body sizes and ecotypes. The first definitive Arikareean Gulf Coast sample of *Palaeogale* occurs at Brooksville 2 with some 13 specimens, including several dentaries. *Palaeogale* is a small mustelid-like taxon,

but it is uncertain if it is more closely related to the feliforms than to the caniforms. This species has a hypercarnivorous dentition and presumably had a diet similar to that of modern weasels consisting almost entirely of small mammals.

There are two new genera and species of musteloids with mesocarnivorous dentitions suggesting that they were omnivorous and, like many present-day mustelids, fed on a variety of foods depending on the season (Ewer, 1973). The first new musteloid that is present is the same size as *Palaeogale* and may be similar to *Plesictis* sp. described by Macdonald (1970) in the Wounded Knee Fauna. Four teeth represent a second new, mink-sized genus similar to the European genera *Angustictis* and *Pseudobassaris*.

The most abundant carnivore is *Phlaocyon*. *Phlaocyon* is a small raccoon-sized borophagine canid with a hypocarnivorous dentition. A second large carnivore at Brooksville 2 is the coyote-sized hesperocyonine canid *Osbornodon*, which has a hypocarnivorous dentition with an enlarged M2. The largest carnivore in the fauna is referred to *Enhydrocyon* although its presence is recorded from a single tooth. A large hypercarnivorous carnivore is not present in this fauna.

The equid found in the Brooksville 2 LF is the same species as occurs at Cow House Slough LF of Florida. Morgan (1993) referred the Cow House Slough LF equid to *Miohippus* sp.; however, this is questionable because the ectoloph connects to the metaloph on the molars, a derived trait not often found in *Miohippus*. Prothero and Shubin (1989) listed this character as a synapomorphy uniting the Anchitheriinae with the Equinae, subfamilies of later more derived horses. The most advanced described *Miohippus*, *M. equinanus*, only occasionally shows this condition. The Cow House Slough and Brooksville 2 equids appear at the time of transition between earlier *Miohippus* and later *Archaeohippus* and *Parahippus* (horses common in the Thomas Farm LF) (Prothero and Shubin, 1989). The Brooksville 2 and Cow House equids probably are transitional forms that have features of both advanced *Miohippus* and primitive *Archaeohippus*. However, because the Brooksville 2 and Cow House Slough teeth show more primitive characters, like absence of plications on the metaloph and more conical protocones, these teeth are conservatively referred to *Miohippus*.

The three artiodactyls preserved in the fauna are a rare oreodont, a small species of *Nanotragulus*, and a small common species of *Nothokemas*. The Brooksville 2 oreodont is close to the oreodont in the White Springs LF (Morgan, 1989). The taxonomy of oreodonts is largely determined by cranial characters, and with only sparse

dental material from Brooksville 2 does not warrant an assignment. The *Nanotragulus* material falls, like the Buda *Nanotragulus*, within the smallest size group (IV) of Frick (1937). Included in this group are the species *N. loomisi*, *N. lulli*, and *N. intermedius*. Frailey (1979) argued that these species were synonymous and by priority all should be placed in *N. loomisi*. Tedford et al. (1996) recognize *Nanotragulus loomisi* as first appearing at the beginning of the Arikareean and extending into "medial" Arikareean. The Buda dentitions differ from the *Nanotragulus* from Brooksville 2 in having more elongate teeth but similar widths. The Brooksville 2 *Nanotragulus* may be a more primitive population, but following Frailey (1979) I have referred it to *N. loomisi*.

The third artiodactyl found at Brooksville 2 represents *Nothokemas waldropi*. In his study of SB-1A, Frailey (1978) named *Nothokemas waldropi* as the smallest species of the genus and suggested that this new species was an Arikareean ancestor to the Hemingfordian *Floridatragulus* and *Nothokemas floridanus*. Later, in his paper on the Buda LF, Frailey (1979) referred small artiodactyl material in the fauna to Camelidae n. gen. et sp. He refrained from further analysis of the sparse sample; however, he did suggest that this sample was allied to a group comprised of *Nothokemas*, *Oxydactylus*, *Gentilicamelus*, *Floridatragulus*, and *Miolabis*. Comparison of *Nothokemas waldropi* with the Buda Camelidae n. gen. et sp. and the Brooksville 2 *Nothokemas* indicates that they all are members of the same genus, if not species. There is a small size difference among samples from the faunas, yet their overall morphology is similar, hence the referral of the Brooksville 2 camel to *N. waldropi*. In addition to the above local faunas, the small species of *Nothokemas* is also found in the Cow House Slough LF and the Franklin Phosphate Pit No. 2 LF. With these new occurrences, *Nothokemas* is recognized as the most common artiodactyl of the Florida Arikareean.

TAPHONOMY

The Brooksville 2 Local Fauna was partially recovered from a series of karst deposits in the Suwannee Limestone. Animals can use such features as living quarters or karst may form deadly traps (Behrensmeyer and Hook, 1992). This taphonomic analysis relied on five lines of evidence: physical condition of the bones, relative representations of the bones, faunal composition, bone orientation, and sediment composition (Pratt, 1989).

The majority of the postcrania recovered show several types of physical modification. Many of the larger bones exhibit evidence of processing by carnivores with

punctures and other direct signs of mastication. Some of the rodent teeth and small carnivore teeth show evidence of acid etching in digestive tracts. The enamel of these teeth has a powdery appearance, whereas teeth abraded by water tend to have a polished surface (Pratt, 1989). In all the sites bones show some evidence of fluvial transport. Site 1B in particular has bones that exhibit extensive modification by water abrasion, scoring a stage 3 of Hunt's (1978) classification, where 0 is the least worn and 3 is the most worn. Sites 1A and 1E show the least amount of transport with bones classified as less than 1. None of the postcranial elements were articulated and much of the dental material consisted of single teeth with the roots broken. Teeth from site 1B were significantly more degraded than those in 1A and 1E. Sites 1A and 1E had the best-preserved materials, which include complete mandibles retaining teeth, and many complete postcranials of the smaller vertebrates. The majority of the complete jaws and also the intact postcranials belong to the chiropterans. This suggests that they were transported very little compared to the other mammals in this deposit. In contrast, most of the larger mammals were represented by extensively broken skeletal material and isolated teeth.

The relative representations of skeletal elements lead to some general conclusions. Long bones, such as tibiae and humeri, were present only as distal or proximal ends. All the complete bones of larger mammals consisted of the most durable compact postcranials such as astragali, carpals, and phalanges. Cranial material, which is often the most delicate of skeletal material, was rare.

Faunal composition shows several different patterns in age distribution, size distribution, and taxa present. The rodents are represented by all age groups. Rodent teeth ranging from very slightly worn deciduous premolars, through unworn molars, to molars that had worn down through all the enamel have been recovered. The bats tend to be younger animals with lightly worn teeth. The rabbits, beavers, and larger mammals display a broad distribution of age classes, but the majority are either young or old animals indicated by unfused epiphyses of the postcranials, deciduous premolars, and unerupted molars for the young individuals, or by heavily worn teeth and degraded skeletal articular surfaces for the old.

The faunal remains at Brooksville 2 show an absence of such larger herbivores as rhinos, anthracotheres, chalicotheres, and tapirs that are often found in similar age faunas of the Great Plains and in some of the other Florida Arikareean faunas. Large carnivores are also absent from Brooksville.

The species present in the fauna also provide information as to the mode of occurrence of the bone accu-

mulation at the sites. The chondrichthyans are typical of those found in the early Eocene and are therefore a re-worked component. Sirenians and kinosternid turtles are exclusively aquatic animals, so their presence along with frogs and crocodilians indicates the existence of nearby water either as lacustrine sinks or cave ponds. The abundant chiropterans are often common cave dwellers, which suggests that the karst features were more cave-like than open-sided sinkhole traps. The near absence of birds could be taken as further evidence that this fauna accumulated in caves rather than in an open sink. The numbers of predator species relative to prey species is high in the Brooksville Fauna with seven carnivores and approximately twenty possible prey taxa. This suggests that at various times caves and hollows in the limestone were used as carnivore denning sites.

From the above evidence, several conclusions about the accumulation of the Brooksville 2 LF can be drawn. The animals of the fauna are parautochthonous, that is they have been "transported from the death or discard site but have stayed within the original habitat" (Behrensmeyer and Hook, 1992:19). Most of the larger ungulate species, *Nanotragulus*, *Nothokemas*, *Miohippus*, and some of the smaller taxa are the result of accumulation by carnivores. Absence of the relatively very large ungulates is due to the limiting factor of prey size that confronted the carnivores utilizing the karst system.

The overall importance of carnivore activity is difficult to gauge, because some modifications, such as disarticulation and preservation of the denser skeletal elements, can be produced either by water transport or by carnivores. In view of this ambiguity, the age distribution of the rodent population, and the lack of digestive modification of many of the rodent teeth, it is proposed that many of the smaller taxa of the fauna, including the bats, actually inhabited various parts of the karst system. The evidence of the increased degradation of the samples from 1B (located in the bottom of the quarry) in comparison with 1A or 1E (located near the top of the quarry) and that bones from all the sites shows evidence of water transportation implies that the Brooksville 2 sites were catchment basins within a larger system of anastomosing solution pipes. Site 1B has the lowest elevation of these basins. This system of pipes may also have acted as a taphonomic filter preferentially transporting certain elements, either through size restriction of the karst pipes or as a result of hydraulic transport factors. Such mechanisms account for the great richness of these samples in relation to the volume of surrounding sediments.

Site 1B was submerged during most of the collect-

ing trips, so excavation of the site was conducted blindly and stratigraphic information was not preserved. Screen-washing provided abundant evidence that the material from that site underwent the most transportation and abrasion. Site 1B contained the largest and most numerous clasts of the surrounding limestone, and the largest percentage of reworked fossils of any of the Brooksville 2 sites. These clasts were subrounded to rounded, whereas 1A and 1E contained more angular detritus.

Sites 1A and 1E were collected in place, so their stratigraphy was preserved. The sediments were deposited in thin laminae, with layers of alternating sand- or silt-size particles and brown to greenish clays. The fossils were preserved in association with the sandier lenses rather than heterogeneously mixed within the sediments. Grain size analysis showed that 91% of the sediment was greater than medium silt to clay size (6ϕ of the Udden-Wentworth scale). Medium to fine ($3-5\phi$) well-rounded quartz sand comprised 4% of the total weight. Limestone pebbles to granules (-1 to -3ϕ) comprised another 1%. Fossil vertebrate remains and fragments of reworked echinoids (-4 to -5ϕ) comprised the final 4% of the total weight. This evidence suggests that at times of higher water flow the vertebrates were washed in along with the sand and silt derived from the calcarenaceous Suwannee Limestone, and then subsequently covered by clay derived from weathering of the limestone. The clay settled from suspension during times of lower flow or from standing water.

Site 1C was a spoil pile, so no original features were left. The sediments that contained the fossils consisted of grayish clay and pebble- to gravel-size chert; very little limestone was present. Site 1C was the only site that produced intact associated materials, like the *Osbornodon* palate. Clearly, the taphonomic processes that formed 1C were different from the other sites, but because the sediment was displaced its origin is dubious. While sediments from site 1D were similar to those of 1A, 1B, and 1E, they did not appear to be in place, so this site also was unsuitable for stratigraphic or sediment analysis.

In summary, the Brooksville 2 LF animals used a system of karst features as dens or burrows in which they and their prey accumulated. As the karst terrain evolved some of the remains were transported through solution pipes to be redeposited subaqueously in the larger fissures of sites 1A, 1B, and 1E. There is no compelling evidence to indicate that the fossil accumulation of any of these sites spanned a significant interval of geologic time. The facts that the taxa are all similar for each of the sites and variation within the more numerous taxa is not broad implies that the time of accumulation was of

relatively "short" duration, less than a million years. In this regard, Brooksville 2 LF resembles most of Florida's other early karst sites (Patton, 1969; Frailey, 1978, 1979; Pratt, 1990).

SYSTEMATIC PALEONTOLOGY

Order INSECTIVORA Illiger, 1811

Superfamily SORICOIDEA Fischer de Waldheim, 1817

Family GEOLABIDIDAE McKenna, 1960

Genus *CENTETODON* Marsh, 1872

Centetodon magnus Clark, 1936

Figure 4, Table 2

TYPE.—PU 13835, right mandibular fragment with p4-m3

OCCURRENCE.—Uintan-late?Arikareean, Great Plains, Wyoming, and Montana; "medial" Arikareean UBI, Florida

REFERRED MATERIAL.—UF 156389 RM2, UF 163561 Lm2

DESCRIPTION.—The M2 from Brooksville 2 LF is 4-rooted, broad transversely, with strong anterior and posterior cingula and broad stylar shelf. The metacone and paracone are subequal in size but the paracone is taller. The protocone is wide and as tall as the paracone. The anterior slope of the protocone is steeper than the posterior slope. The postprotocrista is lower than the preprotocrista and separated from it by a deep talon basin. The parastyle is the largest of the stylar cusps, standing separately from the paracrista that ends at the base of the parastyle. The parastyle is joined with a broad paracingulum that extends upward to become the preprotocrista. A small metastyle is confluent with the metacrista. A strong metacingulum widens between the metastyle and the metacone, thins at the metacone, and joins with the postprotocrista. A metaconule is present midway along the post protocrista where a small ridge from the base of the metacone extends to and merges with the postprotocrista. The paraconule is absent. The posterior cingulum is the widest of the cingula surrounding the protocone, beginning at the lingual base of the metacone and ending at the hypocone. The anterior cingulum begins at the lingual base of the metacone and ends in a small cusplule. These cingula do not join around the lingual tip of the protocone. The two lingual roots extend upward subparallel to each other. The hypoconal root is the larger of the two lingual roots, while, of the two buccal roots, the paraconal root is the larger. The buccal roots are located on the anterior and posterior corners of the stylar shelf.

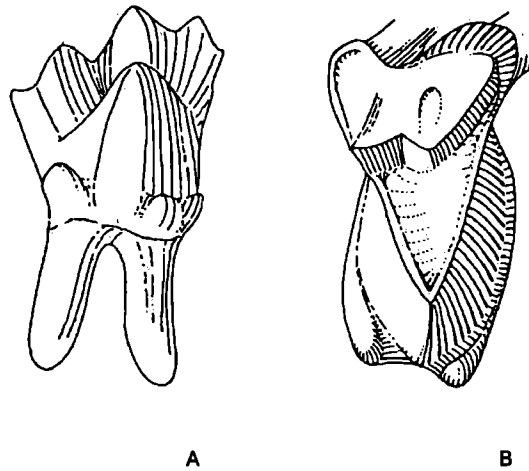


Figure 4. *Centetodon magnus*, x12, UF 156389, RM2. (A) lingual view; (B) occlusal view.

The only lower tooth of *Centetodon* from Brooksville 2 is a heavily worn m2. The trigonid is over twice as tall as the talonid. The talonid width equals that of the trigonid but is anteroposteriorly compressed compared to the trigonid. The metaconid and protoconid are of equal height, although the protoconid is more massive. The paraconid is the smallest trigonid cusp. It lies close to the metaconid and is separated from it by a slight furrow. An anterior cingulid begins on the anterior face of the trigonid and descends steeply to the base of the protoconid where it joins with a weak labial cingulid. The labial cingulid becomes stronger at the hypoflexid. The labial cingulid ends at the anterior base of the hypoconid. The talonid cusps are worn to the point that they form a ridge around the talonid basin. The entoconid region protrudes posterobuccally. There is no posterior cingulid. The cristids are parallel and slanted buccally from the trigonid. The cristid obliquid starts

from the hypoconid region and joins the wall of the trigonid at the middle base of the protoconid. The hypoflexid forms a steep sloped notch ending at the labial cingulid.

DISCUSSION.—The Brooksville 2 specimens match morphologically and fall within the size range for *Centetodon magnus* (Lillegraven et al., 1981). In the Brooksville 2 species the lingual roots are not widely spread and are almost parallel. The only two species of *Centetodon* with this morphological character are *C. magnus* and *C. hendryi* (Lillegraven et al., 1981, Fig. 10). *C. hendryi* is known from Eocene deposits and is a smaller species.

The two *Centetodon* species that range into the Arikareean are *C. magnus* and *C. divaricatus* (Korth, 1992). *C. divaricatus* is larger than the Brooksville 2 species and is similar to *C. wolffi* from the Whitneyan and Orellan. Korth (1992) described *C. divaricatus* as the largest species of the genus based on his comparison with *C. magnus*, but failed to include *C. wolffi*, which is larger in all parameters than *C. divaricatus*. Both *C. divaricatus* and *C. wolffi* have widely spread lingual roots as in *C. marginalis* but unlike *C. magnus* and the Brooksville 2 sample.

Albright (1998) listed *Centetodon* from both Cow House Slough and Buda. The Buda specimens, an upper molar (UF97380) and a complete lower molar (UF97381) are also referable to *C. magnus*. The evidence presented here and in Albright (1998) constitutes the first record of *Centetodon* from east of the Mississippi.

TABLE 2.—Dental measurements of *Centetodon magnus* from Brooksville 2 LF.

UF 156389 RM2		UF 163561 Lm2	
ap	1.75	ap	1.67
tra	2.98	apt	.87
trp	2.74	tra	1.32
		trp	1.05

Superfamily ERINACEOIDEA Fischer de Waldheim,
1817

Family ERINACEIDAE Fischer de Waldheim, 1817

Subfamily ERINACEINAE Fisher de Waldheim,
1817

Tribe AMPHECHININI Rich, 1981

Genus *PARVERICIUS* Koerner, 1940

Parvericius montanus Koerner, 1940

Figure 5, Tables 3, 4

TYPE.—YPM 13956, right maxilla fragment with P3-M3

OCCURRENCE.—Arikareean-late Barstovian, Great Plains, "medial" Arikareean UBI, Florida

REFERRED MATERIAL.—UF163563 RM1, UF163564 RM1, UF163565 Rm1, UF163566 Rm1, UF163567 LM2, UF163568 RM1, UF163569 LM1, UF163570 RM1, UF163571 Lm2, from Brooksville 2 LF, Florida

DESCRIPTION.—The M1 is wider than long. The metacone and protocone are subequal and the largest cusps. The paracone and hypocone are of similar size. The metacone is the tallest cusp. The hypocone is the

lowest. The protocone lies slightly posterior to the paracone on the anterior margin. The distance between the protocone and paracone equals that between the metacone and hypocone. A well-developed postmetacrista is directed from the cusp of the metacone to a strong metastylar spur. A slight preparacrista extends from the paracone to merge with a comparatively weaker parastylar spur. There is an almost complete marginal cingulum except for the lingualmost parts of the protocone and hypocone where the cingulum grades into the stylar spurs. The paracone and protocone are linked by a preprotocrista that gently slopes from the cusp of the paracone to the cusp of the protocone. A less well developed postprotocrista joins the metacone to the protocone and is divided medially with a posterolingually oriented crista extending to the hypocone. The postprotocrista ends at the base of the metacone. No metaconule or paraconule is visible, possibly due to the wear stage of the tooth. Three roots are present above the tooth. The lingual root is the largest, anteroposteriorly flattened and trending to the margins of the crown. The buccal roots are equal in size and are situated almost at the buccal margin of the paracone and metacone.

On M2 the protocone, metacone, and paracone are subequal. The hypocone is small and more distinct compared to that on the M1. There is no ectoflexus in the

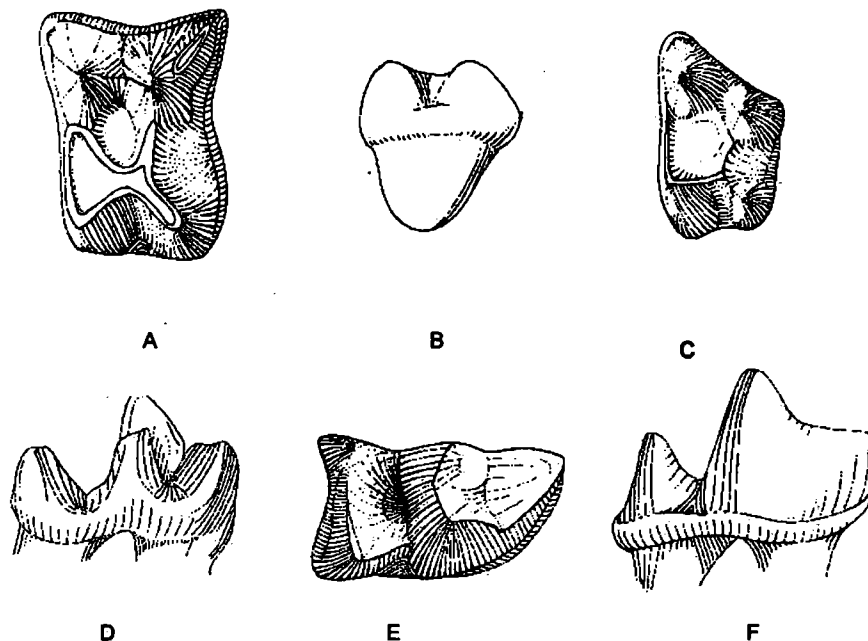


Figure 5. *Parvericius montanus*, x12. (A) UF163569, LM1, occlusal view; (B) UF163569, LM1, lingual view; (C) UF 163567, LM2, occlusal view; (D-F) UF163566, Rm1; (D) lingual view; (E) occlusal view; (F) labial view.

TABLE 3.—Dental measurements of *Parvericius montanus* from Brooksville 2 LF.

M1	(UF163563)	(UF163564)	(UF163568)	(UF 163569)	(UF163570)
ap	2.18	2.10	2.03	1.95	2.00
tr	2.66	2.54	2.46	2.20	2.32
N=5 ap M=2.05 S=0.09					
tr M=2.44 S=0.18					
M2	(UF 163565)				
ap	1.60				
tr	2.08				
m1	(UF 163566)	(UF163567)		m2 (UF 163571)	
ap	2.62	2.52		1.92	
apt	1.51	x		1.12	
tra	1.54	1.48		1.20	
trp	1.72	x		1.08	

buccal margin and, unlike the M1, the buccal margin is slanted mediolingually rather than subparallel to the maxilla. The metacone is moved posteriolingually closer to the hypocone. There is no metastylar spur; the parastylar spur projects buccally rather than anteriorly on the M1 and is now dominant. A paraconule may be present as a thickening in the preprotocrista. A metaconule is part of the postprotocrista. There is a small crista that runs from the base of the hypocone to the metaconule. There are three roots similar to the M1 except that the lingual root is moved above the protocone instead of being equally spaced between the protocone and hypocone, as on the M1.

The trigonid is a little over half the length of the m1. The metaconid is the tallest cusp, the protoconid is the largest, and the paraconid the smallest. The protoconid is pointed anteriorly against the buccal margin. A deep cleft, almost to the base of the crown, separates the metaconid and paraconid from the protoconid. This cleft, on the buccal side, is closed by a paralophid joining the metaconid with the protoconid. A large entoconid and a smaller hypoconid are the only cusps of the talonid. The postcrisid runs lingually from the hypoconid to the base of the entoconid. A narrow buccal cingulid starts from the base of the protoconid and continues to the base of the hypoconid where it joins with a postcingulum. The postcingulum extends upward lingually from the buccal cingulid to merge with the entoconid just above the postcrisid.

The m2 is similar to the m1 except it is 25% smaller and more anteroposteriorly compressed than m1. The

paraconid is reduced and is not distinct from the paralophid. The entoconid and hypoconid are more compressed buccolingually than on the m1 making the talonid more quadrate.

DISCUSSION.—These teeth from Brooksville 2 compare in size and morphology with those of *Parvericius montanus* published by Rich and Rasmussen (1973) and Rich (1981). Korth (1992) described a new species of *Parvericius*, *P. voorhiesi*, that is the same size as *P. montanus*. The new species differs in that the m3 has a posterior cingulid and the P4 has a well-developed parastyle. Since the Brooksville 2 sample contains neither of these diagnostic features, recognition of this taxon is not possible. Korth states that other specimens of the Arikarean age, namely those described by L. Macdonald (1972), might also represent *P. voorhiesi*, but there is no way to know without the defining teeth. I have taken a more conservative approach, questioning the validity of the new species, and assign the Brooksville 2 sample to *P. montanus*.

Rich and Patton (1975) described a hedgehog from the Buda LF as *Amphechinus* sp. because it compared well in size and morphology to the m2 of *Amphechinus horncloudi*. They showed that it was separable from other taxa by describing key differences in similar-sized mammals such as bats and shrews as well as other genera of hedgehogs. However, they failed to make a comparison with *Parvericius*. Although some workers consider *Amphechinus* and *Parvericius* to be synonymous (Macdonald, 1972), Rich recently suggested these taxa are separate. In comparison with M1 from *Parvericius*,

TABLE 4.—Comparison of dental measurements of middle Tertiary Erinaceine hedgehogs with Brooksville 2 LF sample. Compiled from Korth 1992; Rich and Rasmussen 1973; Rich 1981.

	<i>Stenochinus</i>	<i>Paleoscaptor</i>	<i>Amphechinus</i> <i>horncloudi</i>	<i>P. voorhiesi</i>	<i>P. montanus</i>	Brooks- ville 2 LF	Buda
M1 ap	1.7	2.2	3.1-3.4	2.00-2.15	2.0-2.2	1.95-2.18	
tr	2.2	2.6	3.4-3.7	2.38-2.42	2.1-2.6	2.2-2.66	
M2 ap	1.2	1.6	x	x	1.5-1.7	1.6	
tr	1.9	2.2	x	x	1.8-2.2	2.08	
m1 ap	2.0-2.2	2.7	3.6	1.96-2.30	1.9-2.5	2.52-2.62	2.7
apt	1.1-1.4	1.6	2.1	x	1.0-1.5	1.51	1.6
tra	1.1-1.6	1.5	2.3	1.21-1.46	1.2-1.6	1.48-1.54	1.7
trp	1.1-1.7	1.6	2.3-2.4	1.12-1.49	1.3-1.8	1.72	1.6
m2 ap	1.8	1.9	2.7-3.4	1.67-1.90	1.5-1.9	1.92	
apt	0.9-1.1	1.1	1.7-2.0	x	0.8-1.0	1.12	
tra	1.3-1.4	1.4	1.9-2.	1.22-1.26	1.0-1.4	1.20	
trp	1.2-1.3	1.2	1.6-2.1	1.15	0.9-1.4	1.08	

the Buda tooth is only slightly longer and matches in other measurements (see Table 4). Since the Brooksville 2 species has upper molars that are clearly smaller than those of *Amphechinus*, I assign this erinaceid m2 from Buda to *Parvericius* as a m1.

Rich (1981) separates *Amphechinus* and *Parvericius* because *Amphechinus* is larger and has an anteroposteriorly elongated trigonid on m1, whereas *Parvericius* is anteroposteriorly compressed. While it is clear that there is a size difference between the two genera (Table 4), comparisons of measurements of the ratio of overall length to length of the trigonid do not support the second diagnosis. *Parvericius* has a m1 trigonid that is 50-60% of overall length and *Amphechinus*, with fewer specimens, has a m1 trigonid that is 58-60% of overall length. These overlaps in these proportions weakens the distinction between the two genera. I have not proposed formal synonymy here but recommend further investigation of the diagnoses separating *Parvericius* and *Amphechinus*.

Order RODENTIA Bowdich, 1821

Superfamily CASTOROIDEA Gill, 1872

Family CASTORIDAE Gray, 1821

Subfamily AGNOTOCASTORINAE Korth & Emry,
1997

Genus *AGNOTOCASTOR* Stirton, 1935

Agnotocastor sp.

Figure 6, Table 5

TYPE OF GENUS.—*Agnotocastor praetereadens*, Stirton, 1935, AMNH 1428

OCCURRENCE.—Chadronian-early Arikareean, Great Plains; "medial" Arikareean UBI, Florida

REFERRED MATERIAL.—UF143319 Rmlor 2, UF143320 Rm2, UF143321 Lmlor 2, UF143684 Lmlor 2, UF163601 RP4, UF163602 RP4, UF163603 RP4, UF163604 Rp4, UF163605 RP4, UF163606 Lp4, UF163607 Rmlor 2, UF163608 Rmlor 2, UF163609 Rmlor 2, UF163610 Rmlor 2, UF163611 Lmlor 2, UF163612 Rml, UF163613 Lmlor 2, UF163614 RM2, UF163615 RM1or 2, UF163616 RM1or 2, UF163617 RM1or 2, UF163618 LM1or 2, UF163619 RM3, UF163620 Rp4, UF163621 Lp4, UF163622 Ldp4, UF163623 RM3, UF163624 Ldp4, UF163625 Rdp4, UF163626 Rdp4, UF163627 LM3, UF163628 RM3, UF163629 LM3, UF163630 LM3, UF163631 Rdp4, UF163681 upper incisor, UF163752 Lm3, UF163753 M?, UF163754 RM3, UF163755 RM1or 2, UF163756 Rdp4, UF163757 RM3, UF163758 RM1or 2, UF163759 LM1, UF163760 M?, UF175401 lower incisor, UF175402 lower incisor, UF175403 upper incisor, UF175404 upper incisor: from Brooksville 2 LF. UF 40189 upper molar: from Cow House Slough LF.

DESCRIPTION.—This large sample of cheek teeth shows that they are consistently low-crowned. The fossettes are irregularly walled and complex in unworn specimens, becoming smoother and less complex as wear

progresses. The premolars are the largest teeth, while the molars decrease in size from M1/(m1) to M3/(m3). The incisors are small in relation to the cheek teeth.

There are two lower incisors large enough to be referred to as castorid. UF175401 is larger and less degraded than UF175402. Both are smooth surfaced with gently convex enamel faces (Fig. 6:C). Three incisors are referable as upper incisors to Castoridae based again on size and degree of curvature. UF 163681 (Fig. 6:Ca) shows the occlusal surface. UF175404 and UF175403 are fragments of posterior portions. All three are similar, except for larger size, to the lowers with smooth anterior faces that are convex in cross section.

Several deciduous lower and upper premolars were found. They resemble the corresponding P4 in general morphology but are lower crowned, smaller, and have less complex fossettids (Fig. 6:D, E, L).

The p4 is similar to the lower molars except for its larger size. It is also more elongate, and the parafofsettid is more quadrate. In all the lower cheek teeth the hypoflexid is directed posterobuccally and nearly connects with the metafofsettid. The mesoflexid is the same width as the metafofsettid. The mesoflexid's connection to the buccal margin is quickly lost with wear. The parafofsettid is an elongate "S" shape that connects with the mesofossettid in the unworn condition. With wear, the parafofsettid becomes an isolated "L" shape located toward the lingual margin. The m3 is the smallest of the lower teeth and differs from the other teeth in that the mesoflexid tends to completely divide the tooth into a separate anterolophid and posterolophid.

The P4 is larger than the upper molars and similar in morphology except for having a less complex parafofsettid (Fig. 6:M, N). On all upper cheek teeth a deep hypoflexus extends anterobuccally to meet the shallow parafofsettid. The mesoflexus runs from the buccal margin lingually unto the midline where it turns posteriorly to form an "L" shape in slightly to moderately worn specimens. In more worn specimens the posterior portion of the mesoflexus forms a separate hypofossette. In slightly worn teeth a shallow complex metafofsettid lies on the posterobuccal corner. The metafofsettid is usually joined with a smaller fossette that persists longer with wear than the metafofsettid. On the anteroloph of the M1 and M2 a complex parafofsette is present that forms a "Y" shape in less worn teeth and separates into three fossettes with continued wear. The M3 is significantly smaller, by 50-60%, than P4. The posteroloph is compressed transversely and the mesoflexus curves anteriorly, unlike the other molars (Fig. 6:R).

DISCUSSION.—Although there are numerous

early Miocene beavers from the Great Plains (Stirton, 1935; Macdonald, 1963; Martin, 1987) few castorids have been reported from Gulf or Atlantic Coastal Plain regions before the late Barstovian (Hulbert, 1992) and early Clarendonian (Webb et al., 1981). Wood and Wood (1937) listed two teeth as *Palaeocastor* from the Texas Oakville formation (early Miocene) and Albright (1996) described the only significant Arikareean Gulf Coast occurrence of a beaver from the Toledo Bend LF as "*Monosaulax*" *hesperus*.

North American Arikareean *Monosaulax* was reviewed by Korth (1996) and placed into a new genus *Neatocastor*. *Neatocastor* is separate from younger true *Monosaulax* that is associated with later Miocene "*Merychippus* faunas" (Stirton, 1935:416). Korth agreed with Xu (1994) that the two Arikareean species of *Monosaulax*, *M. hesperus* and *M. complexus*, are synonymous. However, the American species were not the same as the Eurasian genus *Stenofiber*. Most recently, Korth and Emry (1997) revised *Anchitheriomys* and placed this genus along with *Neatocastor* and *Agnotocastor* into a new subfamily, Agnotocastorinae. Within this new subfamily, *Agnotocastor* of Whitneyan age is the ancestral genus for Arikareean *Neatocastor* followed by younger *Anchitheriomys*.

The Brooksville 2 sample, although similar in size to *Palaeocastor nebraskensis*, is separable from the Palaeocastorinae and assignable to the Agnotocastorinae as indicated by the comparatively smaller convex incisors and more quadrate cheek teeth. *Palaeocastor* tends to have a shallow mesoflexus that is lost with wear making the cheek teeth more oval shaped. Further, Martin's (1987) partial diagnoses for the Palaeocastorinae, which includes the genera *Palaeocastor*, *Pseudocastor*, *Fossorocastor*, *Euhapsis* and *Capacikala*, is that the incisors are enlarged and flattened and the fossettids are relatively simple, whereas in the Agnotocastorinae the fossettids are more complex and trend toward higher complexity in younger species.

Korth and Emry's (1997) cladistic analysis defines three plesiomorphic characters of *Agnotocastor*, retention of P3, relatively smaller crowned cheek teeth, and less complex fossettids. The lower crown height and less complex fossettids clearly show that the Brooksville 2 sample represents *Agnotocastor*. However, cranial characters rather than dental traits define most genera and species of fossil Castoridae. Therefore, no specific assignment is reached.

As discussed earlier, Albright (1996) referred the only previously described Arikareean Gulf Coast Castorid to "*Monosaulax*" (now *Neatocastor*) *hesperus*. The Brooksville 2 species is significantly

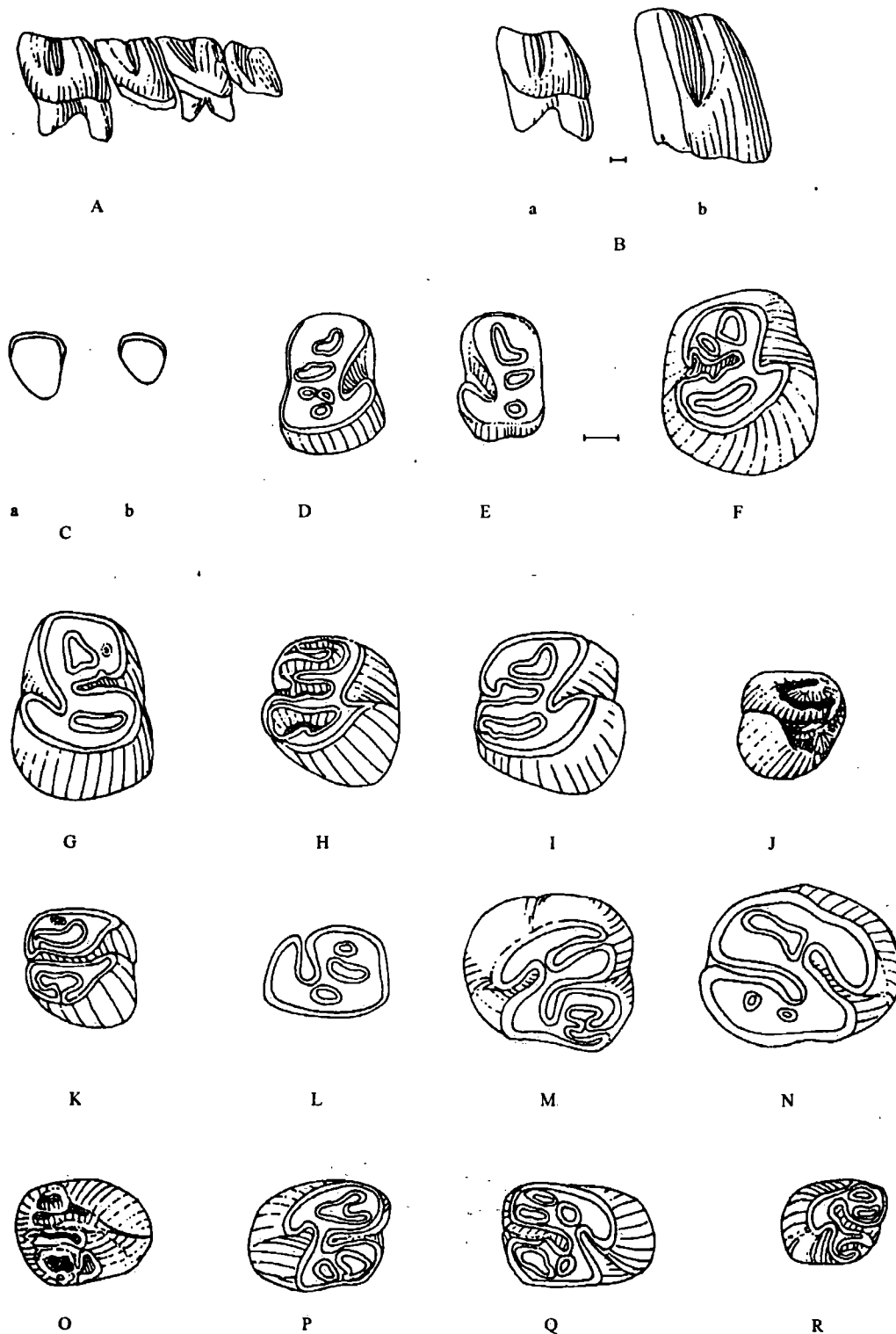


Figure 6. Teeth of *Agnotocastor* sp.: (A) Composite buccal view of Lp4-m3, x3; (B) Comparison of a) BKVL 2 LF Lp4 with b) Toledo Bend LF *Neotocastor hesperus* Lp4, x3; (C) Cross Section of a) upper incisor and b) lower incisor, x3; D-R, magnified x6; (D) UF163631 RDp4; (E) UF163622 LDp4; (F) UF163604 Rp4; (G) UF163606 Lp4; (H) UF163612 Lm2; (I) UF163608 Rm1; (J) UF163752 Lm3, unworn; (K) UF163619 Rm3; (L) UF163756 DP4; (M) UF163601 LP4; (N) UF163603 RP4; (O) UF163758 RM1 or 2, unworn; (P) UF163615 LM1 or 2; (Q) UF163616 RM1 or 2; (R) UF163629 LM3.

TABLE 5.—Dental measurements of *Agnotocastor* sp. from Brooksville 2 LF.

Lower								
incisor	(UF175401)	(UF175402)						
ap	2.9	2.2						
tr	2.6	2.4						
dp4	(UF163631)	(UF163622)	(UF163626)	(UF163625)	N	M	OR	S
ap	3.4	3.2	3.6	3.9	4	3.52	3.2-3.9	0.3
tr	2.6	2.2	2.4	2.4	4	2.4	2.2-2.6	0.16
p4	(UF163621)	(UF163666)	(UF163604)		N	M	OR	S
ap	3.6	4	3.7		3	3.77	3.6-4.0	0.21
tr	3.3	3.5	3.2		3	3.34	3.2-3.5	0.15
m1 or 2	N	M	OR	S				
ap	10	3.03	2.8-3.3	0.21				
tr	10	2.87	2.4-3.2	0.28				
m3	(UF163752)	(UF163619)						
ap	2.6	2.7						
tr	2.1	2.2						
Upper								
incisor	(UF163681)	(UF175404)	(UF175403)					
ap	3	3.3	3.3					
tr	2.9	2.9	2.8					
dP4	(UF163756)							
ap	2.5							
tr	3.2							
P4	(UF163603)	(UF163601)	(UF163602)	(UF163759)	N	M	OR	S
ap	4	3.6	3.9	3.6	4	3.76	3.6-4.0	0.21
tr	4.5	3.8	4.4	3.2	4	3.96	3.2-4.5	0.6
M1 or 2	N	M	OR	S				
ap	8	2.75	2.7-2.8	0.05				
tr	8	2.81	2.6-3.0	0.15				
M3	N	M	OR	S				
ap	7	2.4	2.2-2.6	0.12				
tr	7	2.31	2.2-2.6	0.09				

lower crowned than the Toledo Bend sample (Fig. 6:B) and the fossettoid morphology is not as complex. Following the relationship proposed by Korth between *Neotocastor* and *Agnotocastor*, the Brooksville 2 sample lies near an intermediate stage between the

Whitneyan *Agnotocastor* and the late Arikarean *Neotocastor*.

Hulbert's summary of Florida fossil vertebrates (1992) listed an early late Arikarean castorid from the Cow House Slough LF (UF40189) as indeterminate. This

new sample from Brooksville 2 shows clearly that this specimen is also referable to *Agnotocastor*.

Later occurrences of castorids in Florida include two genera, *Anchitheriomys* and *Eucastor*, found in later Barstovian sediments of the Bone Valley (Hulbert, 1993) and a species of *Eucastor* recovered from the Clarendonian Love Bone Bed locality (Webb et al., 1981). Castorids are notably absent from the Florida record during the late Arikareean, the Hemingfordian, and into the early Barstovian. This absence may be a sampling bias due to the sparseness of samples in localities of these ages.

Order LAGOMORPHA

Family LEPORIDAE Gray, 1821

Subfamily PALAEOLAGINAE Dice, 1929

Genus *MEGALAGUS* Walker, 1931

Megalagus abaconis new species

Figures 7, 8, Table 6

ETYMOLOGY.—*abaconis* (Latin genitive): named for K. Abaco Richardson.

HOLOTYPE.—UF 163640, Lp3

OCCURRENCE.—Brooksville 2 LF, Hernando Co., Florida, "medial" Arikareean UBI

REFERRED MATERIAL.—UF163576 RM3, UF163577 LM1, UF163578 RM2, UF163579 LM2, UF163580 RP4, UF163581 Rm1, UF163582 Lp4, UF163583 Rp3, UF163584 Lm2, UF163585 Lp3, UF163586 RM?, UF163587 RM1, UF163588 M?, UF163589 LP2, UF163590 Lp4, UF163591 Rm2, UF163592 Lp4, UF163593 Lm1, UF163594 Lm2, UF163595 Rm1, UF163596 Rp4, UF163597 LM?, UF163598 Rm3, UF163599 RP3, UF163632 LI1, UF163633 RI1, UF163634 LI1, UF163635 M?, UF163636 LI2, UF163637 RM1, UF163638 RP4, UF163639 Rdp4, UF163641 LP2, UF163642 Lp3, UF163643 Rp3, UF163644 Rp3, UF163645 Rm1, UF163646 Rdp3, UF163647 RM?, UF163648 M?, UF163649 RP2, UF163650 Ldp4, UF163651 Rdp3, UF163652 Rdp4, UF163653 Lm3, UF163658 Ldp3, UF163682 Lm3, UF163683 LM?, UF163684 dP?, UF163685 Ldp3, UF163686 DP?, UF163687 LP4, UF163688 DP?, UF163689 Rp3, UF163690 RM1, UF163691 LM1, UF163751 LM?, UF163766 M3, UF163773 LI1.

DIAGNOSIS.—Advanced *Megalagus*, in which buccal roots on upper molars are reduced and lost quickly with wear. Resembles *Megalagus dawsoni* in greater degree of hypsodonty and cement than older species of *Megalagus* such as *M. primitivus*. Separable from *M. dawsoni* by shorter length of upper molars in relation to

width, and reduction of buccal roots. The p3 has shallow lingual reentrant, lost with slight wear. External reentrant directed anterolingually. Lingual bridge on lower molars forms very late in wear. Lower unworn to moderately worn teeth have crenulated anterior talonid margins. The P2 with reduced buccal lobe. The P3 anteroloph small with crescentic valley open at margin.

DESCRIPTION.—Several lower deciduous premolars have been recovered (Fig. 8:A, B, C, D, E). Deciduous lower premolars of Palaeolaginae have never been described in the literature, so the terminology applied in Fig. 7 is new. A deep transverse valley separates the trigonid into an anteroloph and metaloph. The anteroloph is formed from the paracone and a buccal parastylid. On unworn to slightly worn teeth the anteroloph is lower in height than the metaloph and equal to the talonid (Fig. 8:E). The metaloph consists of the metaconid and protoconid connected by a cristid. A transverse valley separates the talonid and trigonid. A distinctive entoconid is directed posterolingually. A lingual valley divides the entoconid from the mesoconid. The hypoconid lies on the buccal extension of the talonid. The anterior margin of the talonid is narrow and concave. With wear the anterolophid and metalophid join and a central enamel connection forms between the talonid and trigonid (Fig. 8:C).

The holotype of this new species is a single little-worn p3 (Fig. 8:F). The large cement-filled external reentrant has a crenulated posterior enamel surface. The internal reentrant is shallow and disappears quickly with wear. An anterior fold is present that extends minimally down the tooth. In all the p3s the external reentrant is curved anteriorly rather than extending lingually, as in *Palaeolagus philoi*, and the anterolophid is directed posterobuccally. With wear the p3 becomes larger in occlusal outline (Fig. 8:H, I).

The p4-m2 are all similar in size and morphology. The differences among these teeth is the degree of anteroposterior curvature that increases in the posterior teeth. The talonid and trigonid form two separate columns. The trigonid is the larger of the two. In unworn specimens a posterolophid is present on the talonid (Fig. 8:O, P). The trigonid and talonid are connected by cement (Fig. 8:P, Q, R) until very late wear stages when a lingual enamel connection forms (Fig. 8:P, T). The anterior enamel margin of the talonid is thin and crenulated, whereas on the trigonid enamel is absent from the anterior margin. The enamel is thicker on the buccal margin and thins lingually.

The m3 is reduced in overall size with the talonid reduced even more in relative proportions (Fig. 8:P, Q). The m3 is less hypsodont than the other molars.

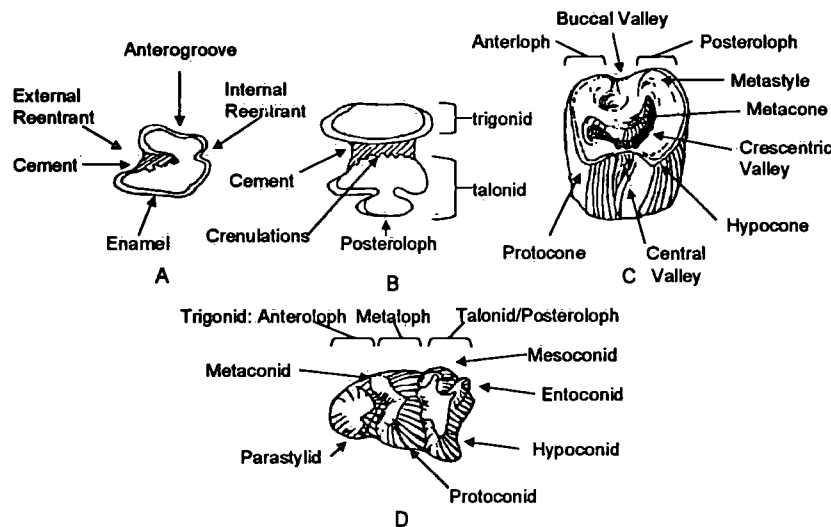
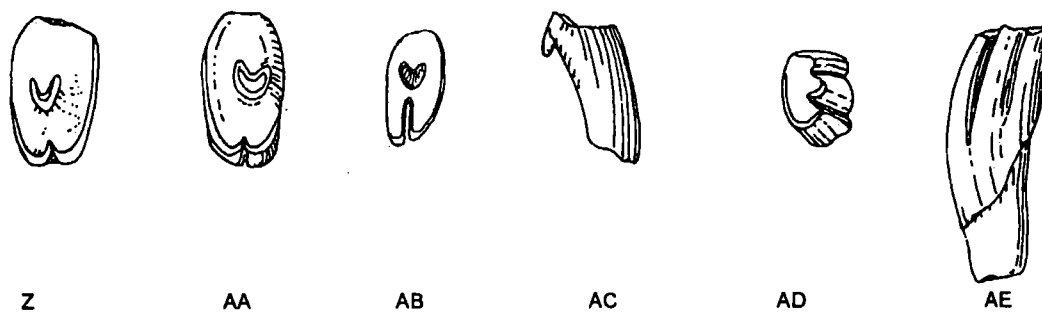
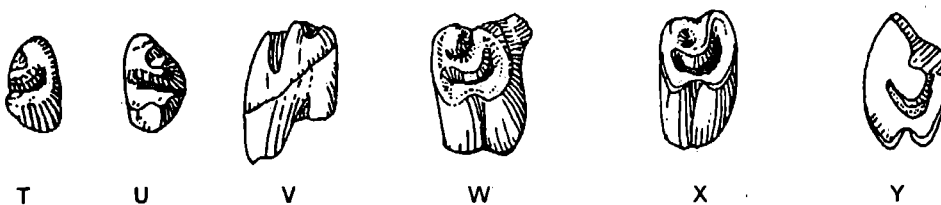
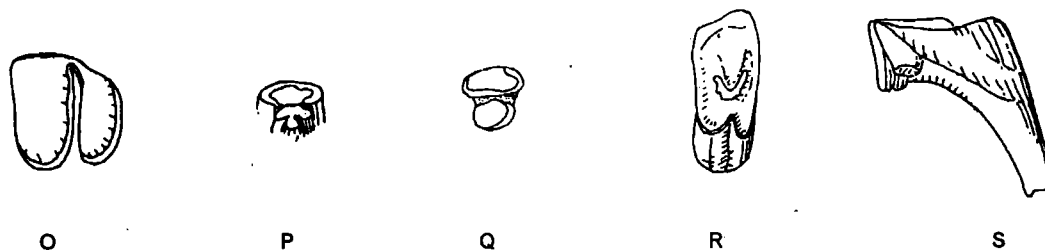
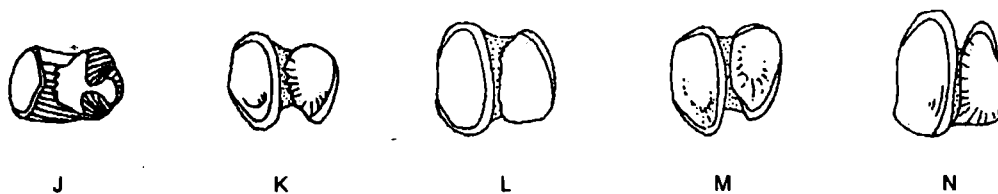
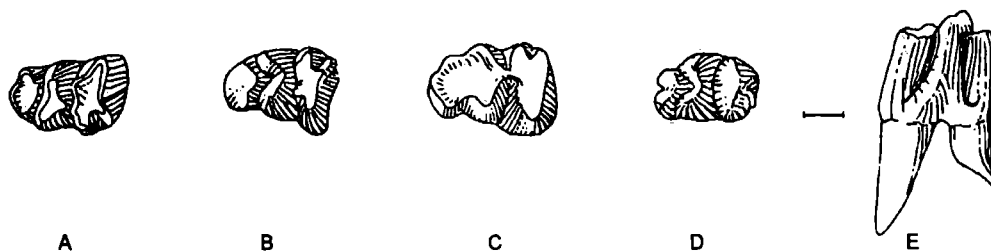


Figure 7. Dental terminology used for Lagomorphs. Partially after A.E. Wood (1940) and Dawson (1958). (A) Lp3; (B) slightly worn lower molar; (C) upper unworn molar; (D) deciduous lower premolar.

TABLE 6.—Dental measurements for *Megalagus abaconis* n. sp. from Brooksville 2 LF.

	N	M	OR	S		N	M	OR	S
dp3/4					I1				
ap	7	2.47	2.3-2.7	0.15	ap	4	2.24	2.2-2.4	0.11
tra	7	1.54	1.5-1.7	0.08	tr	4	1.73	1.5-2.3	0.39
trp	7	1.71	1.5-1.9	0.13					
					I2	(UF163636)			
					ap	1.2			
p3					tr	0.8			
ap	8	2.23	1.9-2.4	0.21					
tr	8	2.12	1.8-2.5	0.27	dP3/4	(UF163687)	(UF163685)	(UF163646)	
					ap	1.7	1.5	1.5	
p4					tr	2.9	2.7	3.1	
ap	4	2.6	2.5-2.7	0.08					
tra	4	2.62	2.5-2.9	0.19	P2	N	M	OR	S
trp	4	2.15	2.0-2.2	0.1	ap	4	1.25	1.1-1.4	0.13
					tr	4	2	1.9-2.1	0.08
m1									
ap	6	2.46	2.4-2.6	0.08	P3	(UF163599)			
tra	6	2.46	1.6-2.7	0.39	ap	2			
trp	6	1.94	1.6-2.1	0.17	tra	2			
					trp	3.4			
m2									
ap	3	2.63	2.6-2.7	0.06	P4	(UF163580)			
tra	3	2.6	2.6	0	ap	2.1			
trp	3	2.23	2.2-2.3	0.06	tr	3.4			
m3					M1/M2	N	M	OR	S
ap	5	1.58	1.1-1.9	0.33	ap	7	1.91	1.8-2.1	0.12
tra	5	1.48	1.3-1.7	0.18	tr	7	3.31	2.7-3.6	0.32
trp	5	1.1	.9-1.4	0.19					
					M3	(UF163766)			
					ap	1.1			
					tr	2			



Both upper incisors have been recovered. There is a single anterior sulcus that divides each incisor into two lobes. The sulcus is located lingually off-center, so the buccal lobe is the largest. The posterior incisor is similar to the anterior incisor except for smaller size and the lack of an internal vascular canal.

The P2 has two anterior reentrants that divide the tooth into three lobes. The buccal lobe is half the length of the lingual lobe. The buccal reentrant is very shallow, while the lingual reentrant extends almost to the crown margin. There are two roots (Fig. 8:T, U, V).

In P3 the anterior lobe is very narrow relative to the posterior lobe. The crescentic valley is open to the anterior margin and the buccal valley is moved inward lingually. The P3 is single-rooted. The central valley is wide and open. The central valley between the anterior and posterior lobes of the upper premolars and first molar is more prominent, while the hypostria is weak or absent. M2 shows the reverse condition with a stronger hypostria (Fig. 8:AB) and less developed central valley.

Buccal roots are present in slightly worn molars although they are small and disappear with later wear. In the fourth premolar buccal roots appear to develop sporadically or perhaps on more developed crowns (Fig. 8:W, X). In unworn molariform teeth the crescentic valley margin is crenulated and a shallow depression lies behind the metacone and lingual to a conical paracone (Fig. 8:W). As the molars wear, the buccal enamel is lost and the lingual enamel at the transverse corners thickens. The crescentic valley enamel wears first to a thick area confined to the metacone region and then wears to a uniform thickness.

The M3 resembles the P2 with two reentrants. However, in comparison with the P2, the reentrants are located on the posterior margin, the lobes are of equal size, and the tooth is higher crowned (Fig. 8:A, E). The M3 is reduced relative to the other molars. The posteroloph is absent and the anteroloph has been compressed posterotransversely.

DISCUSSION.—Lagomorphs have not been described in detail from the Arikareean of the southeastern United States or Florida. Morgan (1989) listed

?*Palaeolagus* in the White Springs LF. On this basis, Hulbert (1992) listed the *Palaeolaginae* as ranging through the late Oligocene into very early Miocene in Florida. Like the beavers, rabbits are curiously absent from the Florida record from the late Arikareean (c.21 Ma) until the late Barstovian (15 Ma) when *Hypolagus* appears (Hulbert, 1992).

Elsewhere, there is a diversity of Arikareean lagomorphs (Wilson, 1949; Dawson, 1967; Stevens et al., 1969; Korth, 1992) with three genera of leporids, *Palaeolagus*, *Archaeolagus*, and *Megalagus*, and two genera of ochotonids, *Gripholagomys* and *Desmatolagus*. These genera are not all present at the same time interval during the Arikareean. *Palaeolagus* disappears after the early Arikareean to be replaced by its descendant *Archaeolagus* (Tedford et al., 1996). *Megalagus* is represented in the Arikareean by two species: *M. primitivus* from the Harrison Formation of Wyoming (Dawson, 1967) and *M. dawsoni*, described by Black (1961) from the Fort Logan Formation of Montana.

The Brooksville 2 rabbit is separable from the Ochotonidae by the possession of lower and upper M3s. In some morphological characters and size (Table 7) the Brooksville 2 sample resembles the advanced *Palaeolagus philoi*. Both have crenulated anterior margins on the talonid and the p3 produces a single reentrant with slight wear; this feature is also found in younger *Archaeolagines*. However, all species of *Megalagus* possess these characters, which are probably convergent with the *Palaeolagus-Archaeolagus* lineage. The retention of buccal roots, primitive P3, and relation of valleys and hypostriae on the upper molars serve to differentiate the Brooksville 2 *Megalagus* from *Palaeolagus* and *Archaeolagus*.

Except for its smaller size, the p3 compares well with those of *Megalagus brachyodon* and *M. primitivus* depicted by Dawson, 1958:17, Fig. 7a. *Megalagus* species tend to have an external reentrant that extends anterolingually and a posteroloph that is directed conversely to the reentrant. *Palaeolagus* and *Archaeolagus* that have a single external reentrant tend to have it lingually directed with a more oval shaped p3. A lower

Figure 8. *Megalagus abaconis* n. sp., x6 scale bar = 1 mm. (A) UF163693 Rdp3 or 4; (B) UF163651 Ldp3 or 4; (C) UF163652 Ldp3 or 4; (D) UF175424 Rdp3 or 4; (E) UF163693 lingual view; (F) UF163640 Lp3, holotype; (G) UF163643 Rp3; (H) UF163644 Rp3; (I) UF163642 Lp3; (J) UF163593 Lm1; (K) UF163596 Rp4; (L) UF163519 Lm2; (M) UF163581 Rm1; (N) UF163582 Rm1; (O) UF163582 Lp4; (P) UF163576 Rm3; (Q) UF163598 Rm3; (R) UF163646 RdP4, occlusal view; (S) UF163646 RdP4, anterior view; (T) UF163589 LP2; (U) UF163641 RP2, occlusal view; (V) UF163641 RP2, anterior view; (W) UF163638 RP4?, unerupted; (X) UF163586 RM1?, unworn; (Y) UF163599 RP3; (Z) UF163589 RP4; (AA) UF163637 RP4; (AB) UF163751 RM2, occlusal view; (AC) UF163751 RM2, anterior view; (AD) UF163766 LM3, occlusal view; (AE) UF163766 LM3, posterior view.

dentary, FAM 99266, of "*Megalagus* sp." from the White River Group, preserves dp3 and dp4 that are similar to those in the Brooksville 2 sample. The P3 is typical of *Megalagus*. In *Palaeolagus* the lobes of P3 are nearly of equal width and the tooth is more molariform. The morphology of the lingual portion of the upper molariform teeth is more indicative of *Megalagus* as well. *Palaeolagus* tends to have weak lingual valleys and stronger hypostriae on the anterior premolars and molars whereas the opposite condition is present in *Megalagus* (Wood, 1940).

With the above comparable characters the Brooksville 2 leporid is assignable to *Megalagus*. This brings the total to three species in the Arikareean. *M. primitivus* with its more primitive morphology begins the early Arikareean and then the advanced lines of *M. dawsoni* in Montana and the new Brooksville 2 LF species in Florida extend into the later Arikareean.

Cow House Slough LF produced a number of lagemorph teeth (UF40155-61, 40190) that I am referring to *Megalagus abaconis* because of their corresponding morphology and size. One upper molar (UF40155) has

TABLE 7.—Comparative dental measurements for Whitneyan-Arikareean Leporidae. Compiled from Dawson 1958, 1967; Black 1961; Stevens et al. 1969.

	<i>Megalagus abaconis</i>	<i>M. dawsoni</i>	<i>M. cf.primitivus</i>	<i>M. turgidus</i>	<i>Palaeolagus hypsodus</i>	<i>P. philoi</i>	<i>Archaeolagus acricolus</i>	<i>A. ennisianus</i>
p3 ap	1.9-2.4	no	2.0-2.1	1.76	2.0-2.2	1.9-2.5	1.7-2.1	2.5-2.7
tr	1.8-2.5	data	2.6-2.8	2.14	2	1.9-2.2	1.7-2.0	2.0-2.5
		available						
p4 ap	2.5-2.7	for lower	2.9-3.3	3.28	2	2.2-2.6	2.2	2.4-2.5
tra	2.5-2.9	teeth	3	2.4	2.1-2.2	2.2-2.8	1.8-2.5	2.4-2.8
trp	2.0-2.2	x	2.5-2.6	2.1	1.6-1.8	1.8-2.2	1.9-2.2	1.9-2.4
m1 ap	2.4-2.6	x	3.0-3.2	3.42	2.1-2.3	2.4-2.6	2.0-2.2	2.4-2.5
tra	1.6-2.7	x	2.9	2.8	2.1-2.4	2.2-2.7	2.0-2.4	2.2-2.6
trp	1.6-2.1	x	2.3-2.6	2.45	1.9-2.0	2.0-2.2	1.7-1.9	1.8-2.2
m2 ap	2.6-2.7	x	2.8	3.27	2.1	2.4-2.7	1.8-2.2	2.7
tra	2.6	x	3	2.74	2.1-2.3	2.0-2.6	1.7-2.4	2.6
trp	2.2-2.3	x	2.4	2.25	1.7-1.8	1.9-2.3	1.5-1.9	2.3
m3 ap	1.1-1.9	x	x	1.29	1.3	1.4	1.2-1.3	1.8
tra	1.3-1.7	x	x	1.73	1.2	1.5	1.3	1.5
trp	.9-1.4	x	x	0.9	0.9	0.9	0.8-0.9	1.4
P2 ap	1.1-1.4	1.2	No	No	1	1.5	.9-1.1	1.7
tr	1.9-2.1	2.1	data	data	1.5-1.8	1.9	2.1-2.2	2.4
			available	available				
P3 ap	2	3	for	for	1.8-1.9	3.2	1.6-1.7	1.7
tra	2	2.5	upper	upper	2.0-2.2	3.6-4.0	2.5-3.0	2.8
trp	3.4	3.4	teeth	teeth	2.6-3.4	x	3.2-3.4	3.5
P4 ap	2.1	2.8	x	x	1.6	2	1.6-1.7	1.7
tra	3.4	3.5	x	x	3.3-3.4	4.0-4.2	3.5-3.6	3.5
M1/ ap	1.8-2.1	2.2-2.5	x	x	1.5-1.7	1.9-2.1	1.6-1.7	1.6-1.8
M2 tra	2.7-3.6	3.1-3.3	x	x	2.6-3.1	3.4-3.9	2.9-3.3	2.8-3.1
M3 ap	1.1	x	x	x	0.7	x	0.6-0.7	0.8
tr	2	x	x	x	1.3-1.5	x	1.3	1

an unusual development of buccal roots that extend not from the lower margin but from two different heights starting halfway up the crown.

The single preserved tooth of a lagomorph from the White Springs LF (UF121427) has a well-developed hypostria and crescentic valley like the molars of *Megalagus abaconis*. On the other hand, the tooth is considerably smaller (ap 1.2; tr 2.7) than specimens from Brooksville and Cow House Slough, which suggests that the White Springs rabbit is a different taxon, possibly assignable to *Archaeolagus*.

Order CARNIVORA Bowdich, 1821

CARNIVORA *incertae sedis*

Genus *PALAEOGALE* von Meyer, 1846

COMMENT.—*Palaeogale* is a carnivore of uncertain affinities that has been allied at different times to Mustelidae (Simpson, 1946) and to Feliformia by descent from early Tertiary Viverravidae (Flynn and Galiano, 1982; Hunt, 1989). The confusion over its taxonomic position is because *Palaeogale* has both mustelid and feliform dental features. Among mustelid features is the reduced m2, while feliform characters include a slit-like carnassial notch, loss of metaconid on m1, and presence of a parastyle on P4. Flynn et al. (1988) proposed that *Palaeogale* be placed in Carnivora *incertae sedis* due to its lack of clear synapomorphies with either caniforms or feliforms and their classification is followed here.

Palaeogale minuta

Figures 9, 10, Table 8

TYPE.—MP.SG 706

TYPE LOCALITY.—St. Gerand le Puy, France

RANGE.—late Oligocene-early Miocene

REFERRED MATERIAL.—UF163535 RP4, UF163537 LP4 w/maxilla- alveoli for M1, UF163539 RP3 w/maxilla, UF163540 LP4, UF163544 LP4, UF1636545 RP4, UF163546 Lm1, UF163548 L. mandible w/m1-m2, UF163549 R. mandible w/p3-m1-alveoli for m2, UF163550 L. mandible w/p3-m1 and alveoli for i3,c,p2-p3, UF163692 LP4, UF163718 Lp4, UF163749 L. edent. mandible-alveoli for p3-m2

DESCRIPTION.—The p1 is absent (UF 163550). The p2 is double rooted (alveoli in UF163550). The p3 is transversely compressed and elongate, as are the rest of the lower teeth. The p4 has a posterior accessory cusp and a cingular cusp on the posterior margin. The lower carnassial has lost the metaconid, the talonid is reduced

and unbasined with the cristid obliqua forming a central longitudinal shearing crest that ends posteriorly in a small cusp (hypoconid?), the protoconid is high thin and sharp, the paraconid is positioned anteriorly, thin, and blade-like. A cingulid is not present. UF163548 preserves the only m2. It is double rooted, small, and oval in outline with a low central ridge that is slightly pinched at the middle of the tooth.

The P3 is the first upper premolar in the Brooksville 2 LF sample. It has a small posterior heel and no accessory cusps. The upper carnassial has a deep and slit-like notch separating the strong metacone blade from the posteriorly slanted paracone. The protocone of the P4 is directed anteriorly and falls in line with a sharp parastyle located on the anterolingual corner. A "U"-shaped notch separates the parastyle and protocone. The P4 has a slight lingual cingulum that begins slightly anterior to the posterior margin of the metacone and ends at the carnassial notch. Only the alveoli represent M1. The M1 would have been strongly compressed transversely and was even more reduced relative to the size of the P4 than in the M1 of the older *Palaeogale* sample from the White River Group.

DISCUSSION.—*Palaeogale* is unique in combining the size of a small mustelid with a hypercarnivorous dentition featuring the lack of a metaconid on the m1, transverse compression of all teeth, and reduction of M2. The Brooksville 2 sample exhibits all the characteristic features of *Palaeogale* dental morphologies (Simpson, 1946) and is similar to specimens of *Palaeogale* housed in the American Museum.

De Bonis (1981) reviewed all Eurasian and North American *Palaeogale*. He synonymized *Palaeogale* species into a total of four taxa. The taxonomy was based on size difference, presence of M2, loss of p1, and age of occurrence. He argued that *Palaeogale* was conservative morphologically, had a large size range within species, and that there were insufficient characters used to separate most described species. Simpson (1946) earlier suggested that two species of *Palaeogale* from the Oligocene of Mongolia, *P. ulysses* and *P. parvula* described by Matthew and Granger (1924), might be synonymized in the belief that the smaller group were females and the larger were males, as in many modern mustelids.

The four species of de Bonis were diagnosed as follows: (1) *Palaeogale sectoria* encompasses all known late Eocene and early Oligocene species, is medium sized, and retains M2 and p1; (2) *P. minuta*, the smallest species, is found in the late Oligocene and early Miocene of Europe and North America, has lost M2 and p1, and, while relatively small, has a very large intraspecific size

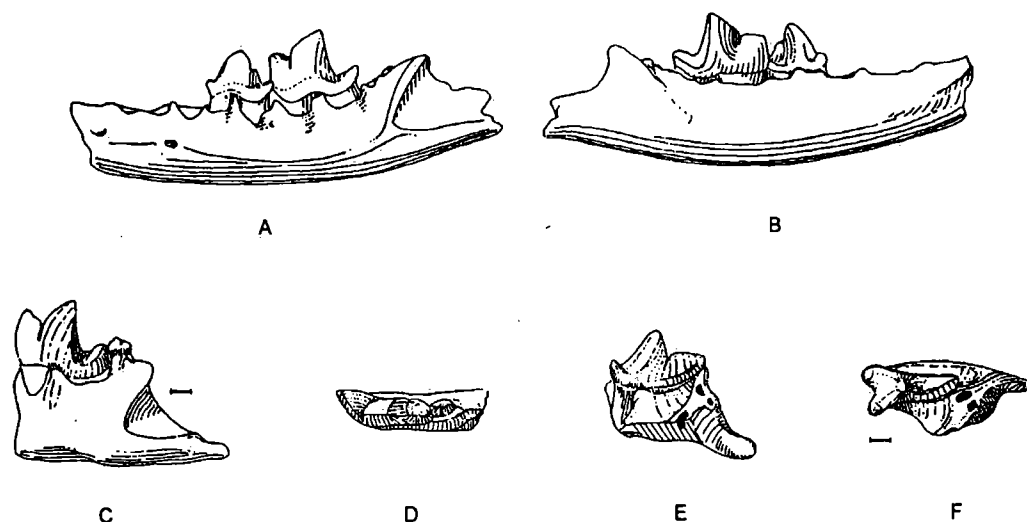


Figure 9. *Palaeogale minuta*, x3, scale bar = 1mm. (A) UF163550, buccal view; (B) UF163550, lingual view; (C) UF163548, buccal view; (D) UF163548, occlusal view; (E) UF163537, lingual view; (F) UF163537, occlusal view.

range with P4s that are 6.5 mm to 3.5mm; (3) *P. hyaenoides*, found only in the Miocene of Europe and medium sized; and (4) *P. dorotheae*, described by Macdonald (1963) in the Arikarean age Wounded Knee fauna of the Great Plains in North America, is also the largest of the *Palaeogale* species.

The Brooksville 2 *Palaeogale* is smaller than most other samples of *P. minuta*. The largest specimen, UF163544, a RP4 with a length of 4.6mm, falls in the lower range of *P. minuta* (see Fig. 10) whereas the smallest, UF163540, also a RP4 with ap=3.25, falls below the range by several tenths of millimeters. Because of

TABLE 8.—Dental Measurements of *Palaeogale minuta* from Brooksville 2 LF.

(UF 163550) (UF 163549) (UF 163548)					(UF 163536)				
p2	alv	1.68	x	x	P3	ap	2.96		
						tr	1.59		
p3	ap	alv-2.47	2.10	x					
	tr	1.00					N	M	OR S
					P4	ap	7	4.06	3.25-4.81 0.60
p4	ap	2.72	2.92	x		tra	7	1.99	1.19-2.48 0.52
	tr	1.28	1.28	x		trp	7	1.48	1.34-1.86 0.37
m1	ap	3.95	4.32	3.81					
	tra	1.41	1.51	1.47					
	trp	0.94	1.02	1.22					
m2	ap	x	x	1.05					
	tr			0.62					
		N	M	OR	S				
m1	ap	6	3.99	3.18-4.61	0.48				
	tra	6	1.35	1.12-1.51	0.15				
	trp	6	1.09	.93-1.24	0.14				

the extensive size range of *P. minuta*, as described by de Bonis, I am referring the Brooksville 2 sample to *P. minuta*. It is possible that the Brooksville 2 *Palaeogale* is an even smaller species that is more hypercarnivorous. Recovery of the M1 might show that the Brooksville 2 sample has a greater reduction of this tooth compared to other species of *Palaeogale*.

Albright (1996) described a partial P4 (LSUMG V-2246) from the Toledo Bend LF as ?*Palaeogale* sp. His referral to *Palaeogale* centered on the presence of a carnassial notch. In modern mustelids the carnassial notch is lost and the metacone blade is not separated from the paracone. This tooth differs from *Palaeogale*, however, and may best be referred to the family Mustelidae, for the reasons below. While eumustelids have lost the carnassial notch, mustelids that are known from the Oligocene to early Miocene, often informally called "palaeomustelids" (Baskin, 1998b), tend to retain the notch but develop mustelid features in the upper and lower molars. As Albright noted, the tooth is most nearly comparable to specimens in the Frick collection of the American Museum labeled "*Miomustela*" that retain a metaconid on the lower carnassial and thus are closer to modern mustelids. Finally, the Toledo Bend speci-

men has an extensive lingual cingulum similar to mustelids, whereas *Palaeogale* has only a slight cingulum under the lingual metacone.

The Brooksville 2 sample marks the first substantial occurrence of *Palaeogale* in the Gulf Coastal Plain. De Bonis (1981) listed a few small, undescribed Hemingfordian specimens from the plains region of North America as *P. minuta*. These specimens are probably congeneric with the Brooksville 2 taxa although they are slightly larger. He found no records or specimens other than *P. dorotheae* (Macdonald, 1963) that are Late Oligocene in age. This author observed a m1 trigonid of *Palaeogale*, AMNH 81039, from the lower Harrison formation (early late Arikareean? of Tedford et al., 1987), that is comparable to the Brooksville 2 *Palaeogale*. There are also undescribed specimens of *Palaeogale* in the McCann Canyon LF, placed by Korth (1992) in the "early late" Arikareean.

In addition to the Brooksville 2 sample, there are a few specimens of *Palaeogale minuta* from SB-1A LF. They include UF117589, an undescribed right maxilla fragment with P3-P4 and m1 alveoli, and UF163888, a partial LP4.

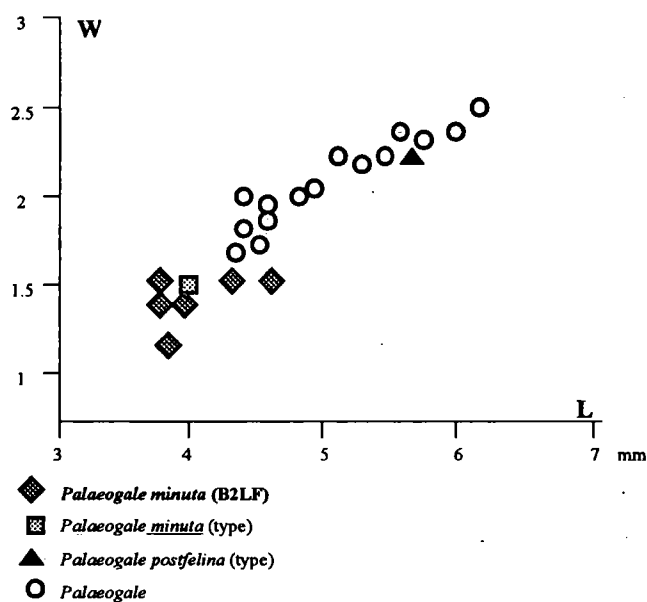


Figure 10. Distribution of m1 as a function of length x width for late Oligocene to Miocene *Palaeogale*. Open Circles are Eurasian samples, open box is *P. minuta*-holotype, closed triangle is *P. "postfelina"*-holotype. The Brooksville 2 LF *Palaeogale* is represented by diamonds.

Suborder CANIFORMIA Kretzoi, 1943
 Infraorder ARCTOIDEA Flower, 1869
 Parvorder MUSTELIDA Tedford, 1976
 Superfamily MUSTELOIDEA Fischer de Waldheim,
 1817

COMMENT.—The record of early musteloids from the Paleogene and earliest Miocene of Europe is quite rich (Helbing, 1930, 1936; Dehm, 1950; Ginsburg, 1961; Lange, 1970; de Bonis and Guinot, 1987; Ginsburg and Morales, 1992; Wolsan, 1993; Cirot and Wolsan, 1994). In contrast, the North American record is sparse. Clark (1936) described the only early North American musteloid, *Mustelavus priscus*, from the late Eocene Chadron Formation on the basis of a single skull and jaws. The next record in North America is in the “early” Arikareean when “*Plesictis*” sp. is reported from the Monroe Creek Fauna (Macdonald, 1970) and *Promartes* appears (Tedford et al., 1987). In the later Arikareean *Oligobunis* appears in North America and throughout the rest of the Tertiary Old World musteloid immigrants continue to invade North America and add to the diversity of the already present taxa (Baskin, 1998b).

The Brooksville 2 musteloids, described below, indicate that the early musteloid diversity in North America is greater than previously known. The Brooksville 2 musteloids may be part of an unknown autochthonous North American radiation derived from *Mustelavus* or they may represent immigrants from Asia that differ from the European musteloids. Unfortunately, the Oligocene record of musteloids in Asia is even less well known than that of North America (B. Wang, 1992), so exploration of the latter hypothesis is not possible. Comparison of the Brooksville 2 material with other Florida localities, SB-1A LF and I-75 LF, and the Toledo Bend LF (see *Palaeogale* discussion) has revealed other early musteloids. These specimens help close the gap between the late Eocene occurrence of *Mustelavus* and the record of *Promartes* and “*Plesictis*” in the late Oligocene.

The radiation of small arctomorph carnivores during the Oligocene and early Miocene may include taxa that are convergent with true mustelids and procyonids but represent non-mustelid and non-procyonid lineages as a part of an undifferentiated stem group whose relationships are controversial (Schmidt-Kittler, 1981; Wolsan, 1993; Wolsan and Lange-Badre, 1996). Alternatively, Baskin (1998a, 1998b) argued that most of the primitive musteloid taxa could be placed in either Procyonidae or Mustelidae on the basis of dental characters. Any musteloids that have a reduced m2/M2 along

with a reduced postprotocrista and metaconule are considered to be mustelids. However, Hunt and Tedford (1993) suggested that features of the auditory region are more reliable for resolving such complex phylogenetic relationships. If there were several radiations of musteloid groups, then dental features may be subject to convergence and may yield misleading phylogenetic hypotheses.

Since no specimens of the Brooksville 2 musteloids preserve the auditory region the relationships of these taxa to mustelids and procyonids is uncertain. Therefore, I do not assign them to either family but recognize that they are part of the early diversity of musteloids.

Because of the rarity of early North American musteloids, I have used Wolsan’s (1993) character analysis of early European musteloids as the framework for discussion and comparison in the systematics. Table 9 is a modified character matrix from Wolsan (1993:350, Table 1) to which I have added two new genera from the Brooksville 2 taxa, *Promartes*, and two more dental features.

Acheronictis webbi new genus and species

Figure 11, Tables 9, 10, 11

ETYMOLOGY.—Genus, *Acheron* (Gr.) river of the netherworld; *iktis* (Gr.) weasel: species, named for S. David Webb

HOLOTYPE.—UF 163745 RM1

OCCURRENCE.—Brooksville 2 LF, Hernando Co., Florida, “medial” Arikareean UBI. ?Monroe Creek F “medial” Arikareean UBI.

REFERRED MATERIAL.—UF163536 LP3 in maxilla frag., UF163538 L. dentary with p2, alveoli for c, p1, UF163547 RP4, UF163703 trigonid Lm1, UF163746 RM1, UF163748 L. dentary with p2, alveoli for c, p1, p3-p4

DIAGNOSIS.—*Acheronictis* is 10-20% smaller than *Mustelavus* and *Angustictis* (Table 11). *Acheronictis* shares the most dental characters with *Mustelavus* and *Mustelictis* (Table 9). Can be separated from *Mustelavus* by the following dental characters: postprotocrista absent; M1 more quadrate (stylar region and anterolingual cingulum wider; transverse width less); M1 protocone lies closer to anterior margin; M1 metaconule variably present (when present it is more distinct than in *Mustelavus*); protocone of P4 less distinct; cingular heel on P3 larger; buccal cingulum on P3 absent; and principle cusps of lower premolars distinguished from *Mustelictis* by smaller size (*Mustelictis* is 30-50% larger).

TABLE 9.—Distribution of the states of 17 dental characters in 12 genera of North American and European mustelidans, new Brooksville 2 LF taxa in boldface. The character states are defined below and follow those of Wolsan (1993: Figs. 4-6, characters 12, 14-27), except for 1 and 2 which are added by this author. An "a" designates the primitive state for each character; "b, c, d, and e" indicate derived states. Polarity of states as defined by Wolsan. In instances in which two different states of the same character could be scored for each genus, both states are listed in the matrix according to the assumed sequence in which they appeared in each genus. Missing data denoted by "?". Characters in brackets are based on extrapolated data. First numbers in parentheses after taxa are characters in common with *Arikarictis* n. gen.; second number italicized in parentheses is characters in common with *Acheronictis* n. gen. All the taxa listed below occur in the late Oligocene and early Miocene, possess a carnassial notch on P4 (*Plesiogale* and *Paragale* have lost this feature), and lack a hypocone on P4.

Taxon	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Stromeriella</i> (5), (8)	a	a	b	a	a	a	b	b	a	a	b	a	a	a	a	a	a
<i>Franconictis</i> (8), (8)	a	a	[b]	b	a	a	a	b	a	c	b	a	a	a	a	a	b
<i>Amphictis</i> (6), (8)	a	a	ab	a	a	a	a	b	a	ac	b	a	a	a	a	a	a
<i>Mustelictis</i> (9), (10)	a	b	b	b	a	a	a	ab	a	ac	b	a	a	ab	a	a	b
<i>Plesictis</i> (7), (5)	c	c	b	b	a	a	b	b	a	de	b	ab	b	b	ab	a	b
<i>Psuedobassaris</i> (7), (9)	b	b	b	b	a	a	a	a	a	ac	b	a	a	b	a	a	ab
<i>Broiliana</i> (4), (6)	a	a	a	ab	a	a	a	b	a	a	ab	a	a	c	a	a	a
<i>Angustictis</i> (7), (7)	b	a	b	b	a	a	a	b	a	c	ab	a	a	c	a	a	a
<i>Mustalavus</i> (6), (11)	a	b	b	a	a	a	a	ab	a	ac	b	a	a	a	a	a	a
<i>Acheronictis</i>	c	b	b	a	a	a	a	ab	a	?	b	a	a	?	?	?	?
<i>Arikarictis</i>	b	c	[b]	b	a	a	a	ab	a	c	[b]	?	?	?	?	?	?
<i>Promartes</i>	b	c	b	b	a	a	ab	b	a	c	b	a	b	b	a	a	b

Definitions of the states of characters: 1 a—postprotocrista present on M1, 1 b—postprotocrista weak on M1, 1 c—postprotocrista absent on M1; 2 a—M1 subequal width metastyle and parastyle region, parastyle only slightly raised, 2 b—M1 metastyle region reduced, height of parastyle less than paracone equal to metacone, 2 c—M1 metastyle region very reduced, height of parastyle equal to or greater than paracone; 3a—P1 two-rooted, 3b—P1 single-rooted, 3c—P1 absent; 4a—P4 protocone not differentiated or crescentic, formed by cingulum entirely, 4b—P4 protocone conical, not formed by cingulum entirely; 5a—P4 hypocone notably smaller than protocone or not differentiated, 5b—P4 hypocone and protocone subequal in size; 6a—M1 larger than or equal in size to P4, 6b—M1 smaller than P4; 7a—lingual half of M1 crown shorter than buccal half, anterior and posterior borders of lingual half not parallel to each other, 7b—lingual half of M1 crown shorter than buccal half, anterior and posterior borders of lingual half parallel to each other, 7c—lingual half of M1 crown about equal in length to or longer than buccal half, halves separated from each other by anteroposterior constriction, 7d—lingual half of M1 crown subequal in length to buccal half, no anteroposterior constriction between both halves; 8a—anterior and posterior cingula of M1 not continuous around lingual base of protocone, 8b—anterior and posterior cingula of M1 continuous around lingual base of protocone; 9a—buccal border of M2 crown situated behind buccal half of M1, 9b—buccal border of M2 crown situated behind lingual half of M1; 10a—M2 three-rooted and distinctly smaller than P4, 10b—M2 three-rooted and subequal in size to P4 (Procyonidae), 10c—M2 two-rooted, 10d—M2 single-rooted, 10e—M2 absent; 11a—p1 two-rooted, 11b—p1 single-rooted, 11c—p1 absent; 12a—m1 trigonid less than three times as long as talonid, 12b—m1 trigonid more than three times as long as talonid; 13a—m1 metaconid distinctly higher than paraconid, 13b—m1 metaconid subequal in height to paraconid, 13c—m1 metaconid distinctly lower than paraconid, 13d—m1 metaconid not differentiated; 14a—m1 entoconid and entoconulid poorly differentiated, anterior and posterior halves of lingual wall of m1 talonid subequal to each other, 14b—m1 entoconid and entoconulid poorly differentiated or not differentiated, anterior half of lingual wall of m1 talonid distinctly lower than posterior half, 14c—m1 entoconid prominent, m1 entoconulid poorly differentiated or not differentiated, 14d—entoconid and entoconulid prominent; 15a—m2 two-rooted, 15b—m2 single-rooted; 16a—m2 metaconid present, 16b—m2 metaconid not differentiated; 17a—talonid basin of m2 distinctly longer than trigonid basin, 17b—talonid and trigonid basins of m2 subequal in length.

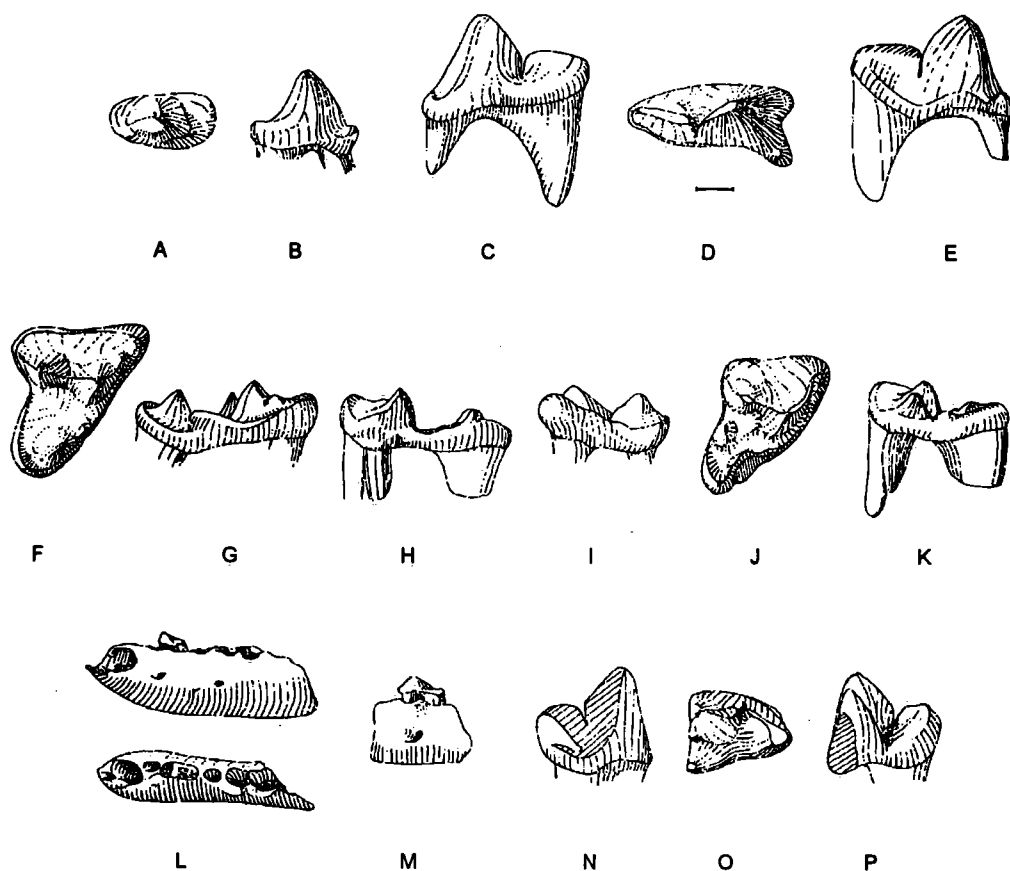


Figure 11. *Acheronictis webbi* n. gen and sp., scale bar = 1 mm. (A) UF163536, LP3, occlusal view; (B) UF163536, LP3, buccal view; (C) UF163547, RP4, buccal view; (D) UF163547, occlusal view; (E) UF163547, lingual view; (F) UF163745, RM1, holotype, occlusal view; (G) UF163745, anterior view; (H) UF163745, posterior view; (I) UF163745, buccal view; (J) UF163746, RM1, occlusal view; (K) UF163746, posterior view; (L) UF163748, L. dentary w/p2, buccal and occlusal views; (M) UF163538, Lp2, buccal view; (N) UF163703, trigonid Lm1, buccal view; (O) UF163703, occlusal view; (P) UF163703, lingual view.

Mustelictis has a much wider M1 in relation to its length. The M1 of *Acheronictis* does not have a postprotocrista unlike *Mustelictis*, *Plesictis*, *Franconictis*, and *Amphictis*. Separable from *Angustictis* by the following: M1 is buccally as long but shorter in width by 20-30%, P3 is smaller in length but broader in width (P3 l/w ratio similar to *Mustelavus* and *Pseudobassar*). *Plesictis* has a more derived stylar region on M1, the metastyle region is more reduced, and the height of the parastyle is greater than the paracone. *Franconictis* and *Amphictis* have a more primitive stylar region, the M1 has a subequal metastyle and parastyle region, and the parastyle is only slightly raised. In *Plesictis* the m1 metaconid is subequal in height to paraconid, while *Acheronictis* has the m1 metaconid higher than paraconid,

similar to *Mustelavus*, *Mustelictis*, and *Amphictis*. P3 similar length to width ratio as *Mustelavus* and *Pseudobassar* but smaller and broader than in *Angustictis*.

DESCRIPTION.—The small protocone on the P4 is anterolingually placed and forms a small subconical heel rather than a distinct cusp (4a). The parastyle is low and elongate as in typical mustelids. A weak lingual cingulum is present and extends the length of the metacone. A weak buccal cingulum was probably present, but wear has made this feature indeterminate. The carnassial notch is present.

The M1 is the most diagnostic of the recovered teeth assigned to this species. The M1 is subtriangular in outline with a broad stylar shelf. The metacone, paracone,

TABLE 10.—Dental measurements for *Acheronictis webbi* n. gen. et sp. (upper and lower teeth) and *Arikarictis chapini* n. gen. and sp. (upper teeth).

		<i>Acheronictis webbi</i>	<i>Arikarictis chapini</i>			<i>Acheronictis webbi</i>
		(UF163536)				(UF163538)
P3	ap	2.9	x	p2	ap	2.6
	tr	1.5	x		tr	1.1
		(UF163547)	(UF163695)			(UF163748)
P4	ap	4.5	7.4	p3	alv	2.7
	tr	2.2	4.3			
		(UF163746)	(UF163702)			(UF163703)
M1	ap	3.1	5.5	(m1)	trigonid	2.9
	tr	3.7	8.1		ap	2
			(UF163745)			
			4.2			
			(UF163699)			
M2	ap	x	1.2			
	tr	x	4.1			

and protocone are subequal in size. The paracone is the tallest of the principal cusps. The parastyle is more developed than the metastylar region (2b). It is weakly connected to the preparacrista and as tall as the metacone. In UF163745 the preprotocrista forms a small distinct cusp before connecting with the paracone (Fig. 11: G). A minute paraconule is distinguishable in the preprotocrista as a slight thickening and notch along the crest. The postprotocrista is entirely absent (1c). The presence of the metaconule is variable: on UF163745 it is absent, while UF163746 has a small conical metaconule

toward the posterior margin. The lingual cingulum is narrow and thickens slightly posteriorly. It is continuous with the posterior cingulum but ends above the buccal protocone margin (8ab). Three roots are present. The lingual is the largest and broad transversely. The buccal roots lie on the buccal margin with the paraconal root larger than the metaconal root. No M2 of this taxon was recovered.

Several lower dentary fragments can be allocated to this genus. The only complete lower tooth that has been recovered is p2, but there is also a trigonid of m1, UF163703. The dentary fragments show that a single

TABLE 11.—Dental measurements for *Acheronictis webbi* n. gen. et sp. and *Arikarictis chapini* n. gen. et sp. from Brooksville 2 LF and other Oligocene-early Miocene musteloids from North America and Europe. Comparative taxa are as follows: A, *Mustelavus priscus*; B *Mustelavus* sp.; C, *Angustictis*; D, *Pseudobassaris*; E, *Mustelictis*; F *Broiliana*; G, *Plesictis genetoides*; H, *Amphictis milloquensis*; I, *Promartes*.

		<i>Achero-nictis</i>	<i>Arika-rictis</i>	A	B	C	D	E	F	G	H	I
P3	ap	2.9	x	3.7	x	3.2	4.5-5.1	4.1	3.7	x	x	x
	tr	1.5	x	1.9	x	1.2	2.5-3.3	2.3	1.8	x	x	x
P4	ap	4.5	7.4	5.2	7.6	4.8-6.0	5.8-7.2	6.5	5.9	7.4	8.5	9.4-10.6
	tr	2.2	4.3	3.8	4.8	2.7-3.4	3.8-5.0	3.8	3.6	4.6	4.6	6.0-6.5
M1	ap	3.1-3.6	5.5	2.9	5.5	3.6-3.7	4.8-6.2	4.2	3.6	4.8	6.2	6.0-6.7
	tr	3.7-4.2	8.1	5.3	7.2	5.2-5.7	6.7-7.8	7.4	6.0	7.2	10	9.8-10.0
M2	ap	x	1.2	x	x	1.8	3.0	x	x	x	x	2.1-2.2
	tr	x	4.1	x	x	3.9	5.7	3.6	x	x	x	5.1-5.6

rooted p1 was present. The p2, UF163538 (Fig. 12: M), is low cusped, posteriorly wider, with the principal cuspid over the anterior root, and a cingular heel over the posterior root. The p2 has weak lingual and anterior cingula. Alveoli for p3 and p4 show that these teeth would be progressively larger and show the same tendency to be wider posteriorly. The m1 trigonid, UF163703 (Fig. 12: N, O, P), has a tall protoconid followed in height by the metaconid (13a) and then the paraconid. The apices of the cusps lie at the margins forming a linguallly open trigonid basin. The paraconid blade forms a deep carnassial notch with the protoconid blade. A small notch is present in the valley between the protoconid and the metaconid. A short buccal cingulid runs from just posterior to the paraconid to the anterior base of the protoconid.

DISCUSSION.—The material assignable to *Acheronictis* is the smallest of any of the early musteloid taxa. It is the same size as *Palaeogale minuta* found at Brooksville 2 (Table 8).

In dental characters *Acheronictis* is closest to *Mustelavus priscus* and the European genus *Mustelictis* (Table 9). This similarity may stem from the fact that dentally *Acheronictis* is not far derived from the plesiomorphic arctoid condition found in *Mustelavus* and *Mustelictis*.

Derived features of *Acheronictis* include the loss of the postprotocrista and enlarged parastyle region, traits shared with many of the advanced late Oligocene European mustelids (Baskin, 1998b). Unfortunately, as discussed under Comment, there is no consensus on musteloid relationships, and convergence of dental traits in *Acheronictis* with the European genera cannot be ruled out.

Acheronictis could be equivalent to “*Plesictis*” sp. (Baskin, 1998b) from the Monroe Creek Fauna (SDSM 6264). They are close in size and morphology. However, since “*Plesictis*” sp. is based on a single fragment of jaw, a sufficient comparison cannot be made to propose formal synonymy.

Arikarictis chapini new genus and species

Figure 12, Tables 9, 10, 11

EYTMOLOGY.—Genus, Arikareean NALMA, *iktis* (Gr.) weasel: species, named for Anne Chapin

HOLOTYPE.—UF163702 LM1

OCCURRENCE.—Brooksville 2 LF, Hernando Co., and SB-1A LF, Suwannee Co., Florida; “medial” Arikareean UBI.

REFERRED MATERIAL.— UF163695 LP4, UF163699 LM2, UF175485 RP4; from Brooksville 2 LF. UF163782 RM2; from SB-1A LF.

GENUS AND SPECIES DIAGNOSIS.—

Smaller than *Promartes* by 20-30%. Larger than *Mustelavus* by 30-35%. *Mustelictis* is 10-20% smaller. Similar in size to *Pseudobassaris* and *Plesictis genettoides* (Table 11). More derived than *Mustelavus* and *Mustelictis* in reduction of postprotocrista and enlargement of parastyle on M1. *Mustelictis* has a more anteroposteriorly compressed M1. *Angustictis* differs by 20-30% larger size of P4 and M1, and 40% lower length to width ratio of M2. On the M1 of *Angustictis* the anterior and posterior cingula are strongly continuous, whereas they are only weakly connected in *Arikarictis*. *Arikarictis* can be distinguished from *Pseudobassaris* by the following dental characters: buccal margin of M1 smaller in comparison to width, M1 hypocone more distinct, M1 posterior margin straight (not recurved towards the anterior), M1 metastyle reduced, M1 parastyle connected to paracone, P4 protocone less robust, and P4 not as elongate in relation to width. Differs from *Plesictis* in having convergent anterior and posterior margins of the lingual half of M1 and two-rooted M2. *Arikarictis* differs from *Broiliana*, *Franconictis*, and *Stromeriella* by more derived postprotocrista, parastyle, and M1 with a more triangular occlusal outline. *Promartes* can be separated from *Arikarictis* by: M1 parastyle not as well-developed into a distinct cusp (higher than paracone), M1 metastyle not as reduced, M1 anterior cingulum weaker, and anterior and posterior margins of lingual half of M1 not parallel (in *Promartes* they are subparallel).

DESCRIPTION.—The teeth that have been recovered from the Brooksville 2 LF are the upper carnassial and molars. P4 retains the carnassial notch. The lingual cingulum begins at the posterior margin of the metacone and ends at the carnassial notch. A ridge runs from the apex of the paracone to a short parastyle close to the paracone margin. The protocone is rounded and anterior of a position directly lingual to the paracone. A buccal cingulum is present along the entire buccal margin but thins along the margin of the paracone.

The M1 has a prominent parastylar region and stylar shelf. The parastyle is as tall as the metacone and formed from the intersection of the anterior cingulum, the buccal cingulum, and the premetacrista. Along the medial to anterior portion of the stylar shelf the buccal cingulum consists of a series of small cusps. The paracone is the tallest of the principal cusps followed by the metacone and then the protocone. The cristae of the transversely compressed metacone and paracone form sharp ridges along the crests of these cusps. The trigon basin is wide and shallow. The paraconule is a slight conical thickening in the preprotocrista and is separated from the protocone by a small notch. The preprotocrista joins

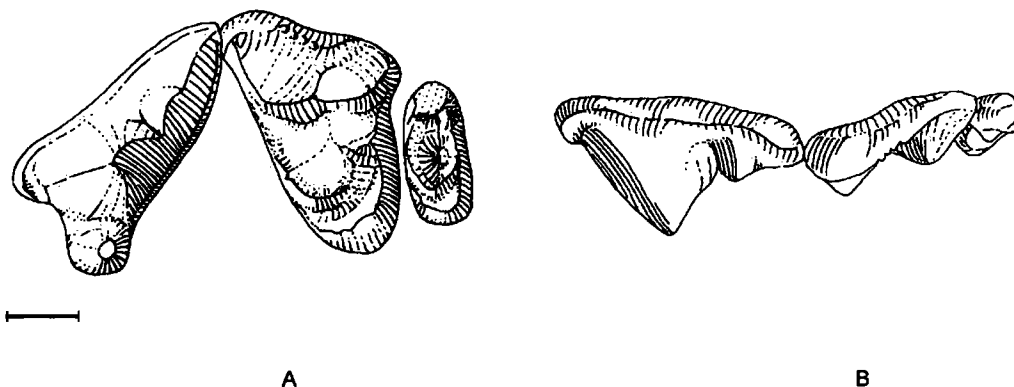


Figure 12. *Arikarictis chapini* n. gen. and sp. UF163695 LP4, UF163702 LM1, UF163699 LM2, scale bar=2 mm. (A) composite occlusal view; (B) composite buccal view.

the more buccal anterior cingulum in front of the metacone. After the paraconule it extends slightly up the slope of the protocone. The postprotocrista is a reduced ridge only at the base of the protocone and at the margin of the posterior portion of the lingual cingulum. The lingual cingulum begins as a minute marginal anterior cingulum above the notch of the paraconule. It thickens and extends in height directly lingual of the protocone, then curves around posteriorly to join with the small but distinct metaconule, and then ends at the base of the metacone. A series of minute cuspules give the posterior portion the appearance of serrations. The lingual cingulum is not continuous with the buccal cingulum.

The M2 is double rooted, half as wide transversely as the M1, and compressed anteroposteriorly compared to the M1. The mid-stylar region is prominent. The paracone is equal in size to the protocone. The metacone is reduced and separated from the paracone by a small central notch. The trigon basin is rounded, depressed upward, and surrounded by a pre and postprotocrista that extend from the centrally located protocone. The lingual cingulum is evenly spaced around the protocone.

DISCUSSION.— Musteloids of this size and morphology have not been described from the Arikarean of North America. Comparison of this taxon with casts of the European musteloids and comparison conducted by Wolsan (written communication, 1998) with the original European specimens shows that the Brooksville 2 material represents a distinct genus.

Table 9 shows that *Arikarictis* resembles many of the European musteloids including *Mustelictis*, *Angustictis*, *Pseudobassaris*, and *Plesictis*. In overall morphology the teeth are closest to *Angustictis* and

Pseudobassaris. These taxa have developed parastylar regions and similar length to width ratios of the M1s. The M2s are also comparably reduced (Table 11). However, as discussed previously, there is disagreement as to the taxonomic placement of the primitive Musteloids. Several species of *Plesictis* and *Pseudobassaris* have been placed in *Mustelictis* (Schmidt-Kittler, 1981) or alternately, *Pseudobassaris* and *Angustictis* have been included in the Procyonidae, as its most primitive members (Wolsan, 1993). Therefore, determination of the precise relationships between *Arikarictis* and other primitive musteloids is not possible at this time.

Infraorder Cynoidea Flower, 1869

Family Canidae Gray, 1821

Subfamily Hesperocyoninae L.D. Martin, 1989

Genus *Enhydrocyon* Cope, 1879

Enhydrocyon cf. *pahinsintewakpa*

Figure 13

TYPE.—SDSM 53325

TYPE LOCALITY.—SDSM V5361, Sharps Formation

OCCURRENCE.—Early to early Late Arikarean; Lower Arikaree Group, Great Plains; "medial" Arikarean UBI, Florida.

REFERRED MATERIAL.—UF163523 LM2

DESCRIPTION.—The M2 has two large roots above the protocone and paracone and a reduced third root above the metacone. The paracone is two-thirds larger than the metacone. The metastylar region is very diminished compared to the parastylar shelf. A thick lin-

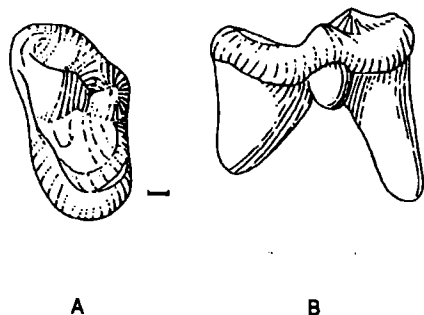


Figure 13. *Enhydrocyon* cf. *pahinsintewakpa*. UF163523 LM2, scale bar = 1 mm. (A) occlusal view; (B) posterior view.

gual cingulum evenly surrounds the trigon basin. The protocone is worn away, its presence indicated by a shallow groove on the posterolingual corner. An anterior cingulum is continuous with the lingual cingulum, thickens in the parastylar region, and ends buccally beside the precentrocrista. The tooth is 4.9mm long and 8.6mm wide.

DISCUSSION.—X. Wang (1994) reviewed the Hesperocyoninae and in his diagnosis of *Enhydrocyon* one of the defining characters is that the lingual cingulum encircles the protocone. Other Hesperocyonines tend to lose all traces of the anterior lingual cingulum on the M2. *Mesocyon* and *Cynodesmus* have a lingual cingulum that is thicker posteriorly and very thin anteriorly. Furthermore, *Cynodesmus* tends to have a broadened buccal region on the M2 with equal sized paracone and metacone. In size the M2 is smaller than that of *Osbornodon* the other medium sized canid present in the Brooksville 2 LF. Comparison with specimens in the Frick collection supports a close alliance to the *Enhydrocyon-Philotrox* clade.

The small metacone and reduced metastylar region are plesiomorphic features found in the older species of *Enhydrocyon* and the sister genus *Philotrox*. The more derived younger species, *E. stenocephalus*, *E. basilatus* and *E. crassidens*, tend to have more equal lingual cingulum and buccal regions. The relative size of the M2 also indicates a primitive form. *Enhydrocyon basilatus* and *E. crassidens*, the terminal members of the group, both have comparatively reduced M2s that are single rooted or in some cases absent (X. Wang, 1994). *Sunkahetanka* and *Philotrox* have the same size M2 as *E. pahinsintewakpa*, but the metacone and metastylar regions are not as reduced in these genera.

Macdonald (1963) originally described *E. pahinsintewakpa*, the most plesiomorphic species of *Enhydrocyon*, as *Sunkahetanka pahinsintewaka*, but X. Wang (1994) placed this species into *Enhydrocyon* based

on the more derived cranial features compared to *Sunkahetanka geringensis*. Since the Brooksville 2 species has the above mentioned primitive features along with a small third root above the metacone, it is appropriate to refer this material to *E. pahinsintewakpa*. However, with only a single tooth upon which to base this assignment, it is appropriate to place a cf. (*confero*) before the trivial name.

Genus *OSBORNODON* Wang, 1994

Osbornodon wangi new species

FIGURE 14, TABLE 12

ETYMOLOGY.— species, named for Xiaoming Wang

HOLOTYPE.—UF 163693, associated RP3-M2:LP4-M2

OCCURRENCE.—Brooksville 2 LF, Hernando County, Florida; “medial” Arikarean UBI.

REFERRED MATERIAL.—UF163696 partial P4, UF163697 incisor, UF163724 m3, UF163743 Canine, UF175476 RP4, UF175477 LP3, UF175480 RM1

DIAGNOSIS.—*Osbornodon wangi* is larger than the Whitneyan species of *O. sesnoni* and *O. renjiei*, and falls within the small end of the size range of the Hemingfordian *O. iamonsensis* (see Table 13). In general, the dentition of *O. wangi* is not as robust as that of *O. iamonsensis*. *O. wangi* can be separated from *O. iamonsensis* on the basis of the following plesiomorphic features that are also found in the older species of *Osbornodon*: the M1 parastyle is more distinct; the premolars are more slender in comparison to the molars and the roots are more gracile.

DESCRIPTION.—The P3 is slender with a low principle cusp, a posterior accessory cusp, and a cingular

cusps. The small P4 protocone is anteriorly placed and is connected to the paracone by a slight crista that forms a minute cuspule on the lingual slope of the paracone. A thick ridge runs from the apex of the paracone to join with the anterior cingulum at the anteromedial margin. A lingual cingulum begins at the posterior of the metacone and ends just anterior of the cusp of the paracone. A slight buccal cingulum appears to start at the posterior of the metacone and connect with the anterior cingulum although part of the buccal margin is broken below the carnassial notch, so the full extent of the cingulum is based on other more complete *Osbornodon* P4s. The lingual surface of the P4 is vertical and flat except for the anterior portion.

The M1 is subquadrate in outline. The paracone is taller than the metacone. Both cusps are subconical with an anteroposterior ridge along the crests. The parastyle almost equals the height of the metacone. It is low and elongate but still distinct as a cusp. The protocone is small and forms a posterobuccally directed ridge connecting with the metaconule by way of the postprotocrista. The preprotocrista extends buccally to just above the paracone. The metaconule continues posteriorly to connect with the posterior cingulum. A well-developed posteriorly directed internal cingulum is present that is continuous with the slight anterior cingulum. The hypocone is separated from the lingual cingulum crest by a small transverse valley on the buccal slope and a conical thickening of the cingulum. Posterior to the protocone, the lingual cingulum reaches the same height as the protocone until past the hypocone. After the hypocone the lingual cingulum rises to the metacone and joins the posterior cingulum.

The M2 is relatively large. The paracone is the largest principle cusp but is less distinct from the metacone than on the M1. The metastylar region is absent and the metacone is reduced compared to the M1. The hypocone and lingual cingulum are large in relation to the size of the M2.

DISCUSSION.—*Osbornodon* has the most exten-

sive time distribution of the Hesperocyoninae. It ranges from the Orellan to early Barstovian, although there is a large time gap during the Arikareean that is devoid of representation (X. Wang, 1994). In geographic range *Osbornodon* is found from the Great Plains to southern regions such as New Mexico and Florida. *Osbornodon* is separated from other Hesperocyonines by two synapomorphies: "antero-posteriorly elongated (thus more quadrate) upper molars and enlargement of M2 and m2" (X. Wang and Tedford, 1996:441). Most of the other Hesperocyonines tend to have reduced M2s like *Enhydrocyon*.

The common carnivore taxon in the famous Thomas Farm locality of Gilchrist Co. Florida is *Osbornodon iamonensis*. This sample was transferred to *Osbornodon* from *Cynodesmus* by X. Wang (1994). In his review *Cynodesmus* was restricted to two species existing from the Whitneyan to the Early Arikareean. The Brooksville 2 material is broadly comparable to the Thomas Farm species although there are some differences. *Osbornodon iamonensis* appears more robust and slightly more derived than *O. wangi*. *Osbornodon renjieii* and *O. sesnoni* have a distinct parastyle while younger species lose the distinct parastyle on the M1. The Brooksville 2 *Osbornodon* is intermediate in this feature. The P4 is enlarged relative to the P3 in younger species but this is not seen in the pre-Arikareean species. The Brooksville 2 *Osbornodon* has a P4 to P3 length ratio similar to *O. iamonensis*, but the P3 has narrower proportions, as in the older species.

Osbornodon is a conservative genus in dental morphology. X. Wang and Tedford (1996) use small size difference and more slender premolars to distinguish *O. sesnoni* from *O. renjieii*. In younger species of *Osbornodon* cranial features become more important in diagnosing species. In light of the differences outlined above, and following the taxonomy of X. Wang (1994), the naming a new species is warranted.

Most of the Arikareean has no representative of the *Osbornodon* lineage. Therefore, the Brooksville 2 sample represents a significant new species that helps fill the

Figure 14. *Osbornodon wangi* n. sp., UF163693, RP3-M2, x1.2.

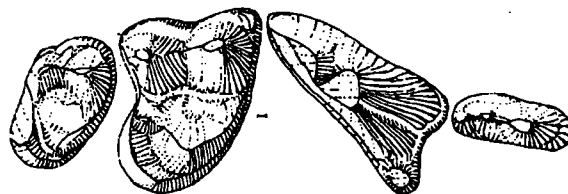


TABLE 12.—Dental measurements of *Osbornodon wangi* n. sp. with closest species of *Osbornodon* for comparison, from X. Wang 1994. Measurements made following X. Wang 1994:17, Fig.6.

		<i>Osbornodon sesnoui</i>		<i>Osbornodon wangi</i>	<i>Osbornodon iamonensis</i>	
		M	OR		M	OR
P4	ap	13.35	13.0-13.7	15.0	18.0	14.6-19.6
	tra	8.6	x	8.0	10.4	8.5-12.2
	trp	15.4	x	16.4	19.44	15.7-21.8
M1	ap	10.1	x	10.6	11.94	10.0-13.3
	tra	13.6	x	15.2	16.93	13.7-18.7
	trp	11.6	x	12.2	14.43	12.2-16.2
M2	ap	6.05	5.8-6.3	6.3	7.0	5.6-8.0
	tra	9.85	9.4-10.3	10.4	11.0	8.7-13.0
	trp	8.3	8.0-8.6	8.8	9.66	7.9-12.0

gap between *O. sesnoui* and younger, larger species of *Osbornodon*.

Subfamily BOROPHAGINAE Simpson, 1948

Tribe PHLAOCYONINI X. Wang et al. 1999

Genus *PHLAOCYON* Matthew, 1899

Phlaocyon taylori new species

Figures 15, 16, Table 13

ETYMOLOGY.—species, named for Eric Taylor

HOLOTYPE.—UF163524 Lm1

OCCURRENCE.—Brooksville 2 LF, Hernando Co., Cow House Slough LF, Hillsborough Co., Florida; "medial" Arikareean UBI

REFERRED MATERIAL.—UF163501 RM2, UF163502 LM2, UF173503 Rm1, UF163504 Lm2, UF163505 RM1, UF163506 RM1, UF163507 RM1, UF163508 Rm1, UF163509 RM1, UF163510 LM1, UF163511 Lm2, UF163512 Lm1, UF163513 RM1, UF163514 LM1, UF163515 Rm2, UF163516 Rm1, UF163517 RP4, UF163519 LP4, UF163520 LM1, UF163521 RM1, UF163522 RM2, UF163525 Lm1 trigonid, UF163526 Lm1, UF163527 RM2, UF163528 m1 talonid, UF163529 Rp3, UF163531 Rp4, UF163533 LP4, UF163534 RP4, UF163701 RM2, UF163716 m3, UF163720 P4, UF163721 P4, UF163724 m3, UF163741 canine, UF163818 LM1, UF163819 LM1; from Brooksville 2 LF. UF40149 Lp4, UF40151 canine; from Cow House Slough LF.

DIAGNOSIS.—Smallest species of the genus (Fig.15). Closest in size to *P. achoros*. Well-developed

metaconule and paraconule on M1. Metaconule twinned on M1 like *P. achoros* and *P. multicuspus*. Paraconule variably twinned. Distinguishable from *P. achoros* by the following features: absent to weakly developed hypocone on P4, lingual cingulum on M1 cuspidate, protostylid absent to minute on m1, accessory cusps on posterior cristid and cristid oblique of talonid m1, and mesoconid present. Differs from *P. multicuspus* by its much smaller size and absence of conical hypocone on M2.

DESCRIPTION.—On P4 the paracone forms a tall enlarged cone. The bladelike metacone is half the height of the paracone with a small division of the central crest. The lingual cingulum is well-developed. The hypocone varies from a thickening in the lingual cingulum (Fig. 16:A) to a minute, but distinct, cusp (Fig. 16:C, D). The anteriorly placed protocone forms a distinct high cusp. A small ridge runs from the apex of the paracone to a low elongate central parastyle that is connected to an anterior cingulum. A slight buccal cingulum is present that ends at the carnassial notch.

The upper molars are cuspidate and quadrate. The paracone is the tallest cusp, followed by the metacone and then the protocone. The paracone and metacone are in line, elongated transversely, and connected together by a "V"-shaped centrocrista. A thick buccal cingulum is present that becomes wider in the parastylar region. On M1 a twinned metaconule is always present and is tripled in some specimens (Fig. 16:G). The paraconule is well developed and usually doubled (Fig. 16:E, F, G). The post-hypocrista extends from the metacone to the posteriorly directed hypocone. The lingual cingulum is prominent with small cusps on the crest. It joins the

anterior cingulum that is continuous with the buccal cingulum at the anterobuccal margin. M2 has a reduced metacone and the metastylar region is absent which makes the buccal margin slant posterolingually. The metaconule is small relative to the M1 and not doubled. The paraconule is also reduced. The lingual cingulum is compressed buccally lingual to the protocone, giving M2 a more oval shape than M1 (Fig. 16:A). A distinct hypocone is not present.

Lower p4 is slender and tall (Fig. 16:H, I). A small cingular cusp lies on the anterior and another on the posterior margin of the tooth. A weak accessory cusp sits high on the posterior slope of the principle cusp. A slight buccal cingulid is present.

Lower m1 is distinctive due to its hypocarnivorous adaptations (Fig. 16:J, K, L). The protoconid is the dominant trigonid cusp. The paraconid lies almost directly anterior of the metaconid. The buccal side of the paracone forms a blade that meets the protoconid at the carnassial notch. The lingual portion of the paraconid is low and open. A slight buccal cingulum runs along the trigonid, beginning just below the paraconid and curving upward toward the posterior protoconid. A weak protostylid occupies the buccal slope of the protocone on the holotype specimen, but is not found on the other m1s. The talonid is basined and cuspidate. A distinct mesoconid lies on the posterior slope of the metaconid.

The entoconid is the dominant cusp and also the most conical of the talonid cusps. Two to three accessory cusps occur on the posterior cristid and the crista obliqua. The hypocone forms the raised posterior buccal corner of the crista obliqua. The crista obliqua is connected to the trigonid wall just buccal to the protoconid-metaconid valley.

A deciduous p4 was recovered and is of proper size and morphology to be assignable to *Phlaocyon taylori*. This dp4 is gracile compared to the permanent m1. The cristid obliquid is absent, so that the hypocone lies next to the trigonid wall. The posterior cristid is slanted posterobuccally with four accessory cusps that enlarge successively toward the posterior end of the premolar.

The m2 differs from m1 in its shorter anteroposterior ratio, enlarged buccal cingulid, small protostylid, and paraconid diminished to the size of the buccal cingulid. All the other cusps are similar to the m1 but changed in proportional size (Fig. 16:M). The m3 is small and circular in outline. Only the metacone and protocone are discernible. They form an indistinct transverse ridge.

DISCUSSION.—In morphology and size *Phlaocyon taylori* n.sp. is close to what Frailey (1979) described as "*Bassariscops*" *achoros* from the Buda LF. In their review of the Borophaginae, X. Wang et al. (1999) recognize two genera within Frailey's hypodigm of *B. achoros*. To the genus *Phlaocyon* they assigned the hypocarnivorous specimens, the holotype of *B. achoros*, and

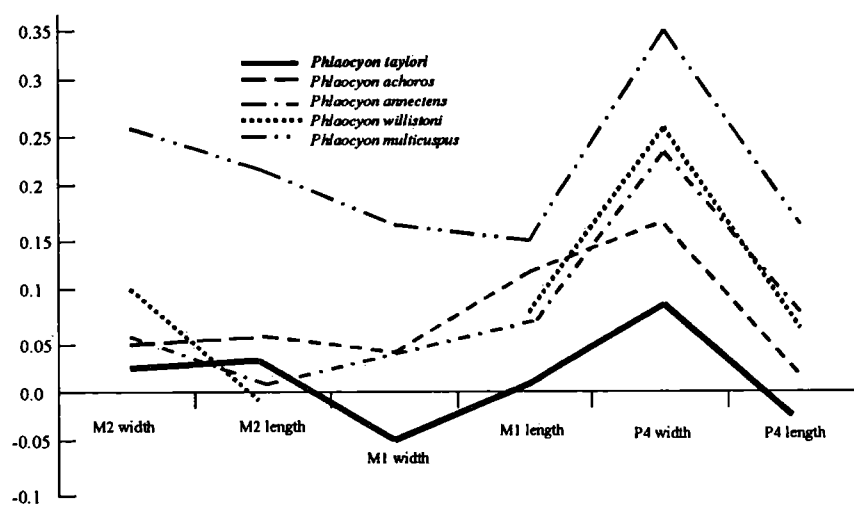


Figure 15. Log differentials of dental measurements among species of *Phlaocyon* compared to *Archaeocyon pavidus* as standard. (Modified from X. Wang et al. 1999.)

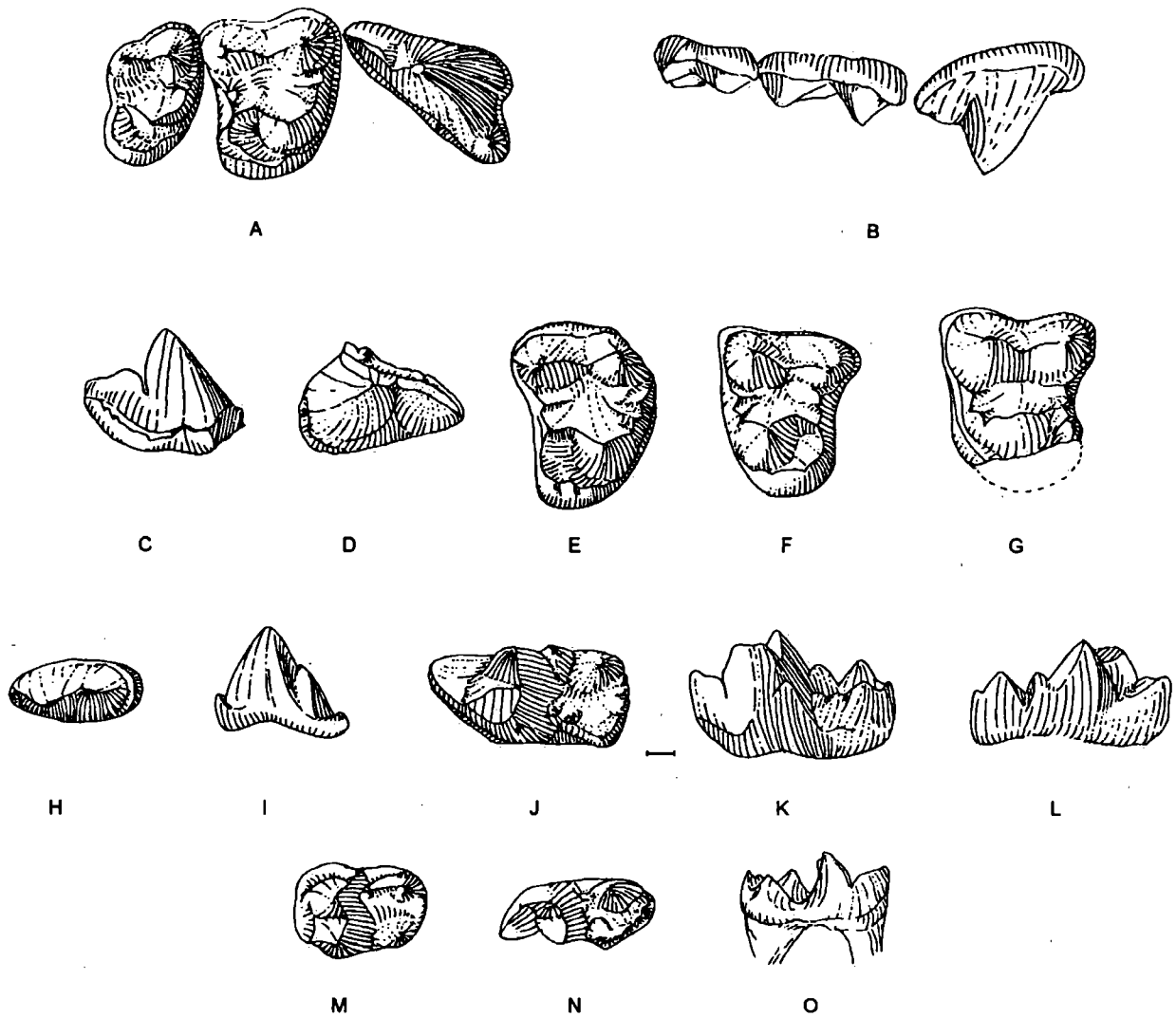


Figure 16. *Phlaocyon taylori* n. sp., x4.5, scale bar = 1 mm. (A) composite, UF163522, RM2; UF163521, RM1; UF163534; occlusal view; (B) composite, buccal view; (C) UF163517, partial RP4, lingual view; (D) UF163517, occlusal view; (E) UF163513, RM1; (F) UF163520, LM1; (G) UF163514, RM1; (H) UF163720, Rp4, occlusal view; (I) UF163720, buccal view; (J) UF163524, Lm1, holotype, occlusal view; (K) UF163524, buccal view; (L) UF163524, lingual view; (M) UF163511, Rm2; (N) UF163700, Rdp4, occlusal view; (O) UF163700, occlusal view.

an m1 Frailey had referred to *Cynarctoides*. These assignments are based on their cladistic analysis of the genus, specifically on shared synapomorphies of these specimens with *P. multicuspus*. They placed the more mesocarnivorous teeth from the Buda LF in *Cynarctoides lemur*.

Peterson (1924) originally included "*Bassariscops*" in *Phlaocyon* when it was considered a procyonid because of its hypocarnivorous dentition. Hough (1948) later demonstrated that *Phlaocyon*'s ear region was essentially canid and Frailey (1979) further solidified this

when he compared the anatomy of the petrosal bone of "*Bassariscops*" *achoros* with those of other taxa and determined that its relationship was clearly with the canids. X. Wang et al. (1999) place *Phlaocyon achoros* within the borophagine canids as part of a hypocarnivorous clade encompassing *Cynarctoides* McGrew, 1938; "*Bassariscops*" Peterson, 1924; and "*Aletocyon*" Romer and Sutton, 1927.

In the new species diagnosis X. Wang et al. (1999) suggest that *P. achoros* is allied to the Hemingfordian *P.*

multicuspus. Even though *P. multicuspus* is much larger, the taxa share several derived features. The twinned metaconule is also shared with *Phlaocyon taylori*. These three species are the only ones to possess this character in the *Phlaocyon* clade, suggesting a separate, more hypocarnivorous lineage within the clade. On the other hand, proposing a direct lineage between these taxa is problematic due to the fact that each possesses derived unique characters of its own and the similarities may be convergent. As stated in the species diagnosis the Brooksville 2 *Phlaocyon* has even more cuspidate molars than the younger *P. achoros*, whereas *P. achoros* and *P. multicuspus* each has a much larger hypocone on P4 and a well defined protostylid on m1. This was not observed in *Phlaocyon taylori* n. sp.

Phlaocyon is a common omnivorous member of the Arikareean faunas of Florida, occurring in four of the seven known localities. Along with Buda and Brooksville, SB-1A has a P4 (TRO 392) that Frailey (1978) described as *Phlaocyon* sp. This upper carnassial has a well-developed hypocone, and therefore prob-

ably represents another species of *Phlaocyon*, rather than the Brooksville 2 LF species. In addition, the sparse carnivore material from Cow House Slough LF indicates the presence of *Phlaocyon taylori* n. sp. on the basis of UF40149, a left p4, and possibly UF40151, a canine. Specimens tentatively labeled *Phlaocyon* (UF163892-96) in the Thomas Farm collection possibly belong to this genus, but more study is needed. If the Thomas Farm material is *Phlaocyon*, it may represent a species derived from a lineage that begins with *Phlaocyon taylori*. This lineage follows a trend of gaining complexity in the P4 and losing complexity in the M1 and M2. The trend might be used in the future for biochronological refinement of stages in the Arikareean and Hemingfordian.

AGE AND CORRELATION

Correlation within the Arikareean NALMA presents some difficulty because there is no currently accepted biochronology for the "age" that spans the interval from

TABLE 13.—Dental measurements of *Phlaocyon taylori* n. sp. from Brooksville 2 LF and *P. achoros* from the Buda LF for comparison.

<i>Phlaocyon taylori</i>					<i>Phlaocyon achoros</i>	
P4	(UF163533)	(UF163534)			(UF18389)	(UF22778)
ap	6.2	6.0			6.8	4.1
tr	3.8	3.3			7.1	4.4
M1	N	M	OR	S	(UF18501)	
ap	11	5.14	4.6-5.8	0.36	6.5	
tr	10	6.19	5.7-6.9	0.38	7.6	
M2	(UF163522)	(UF163501)	(UF163701)		(UF171361)	(UF171362)
ap	3.8	3.8	3.7		4.1	3.6
tr	5.1	5.4	5.0		6.0	4.7
p4	(UF163720)	(UF163721)			(UF171365)	(UF171366)
ap	4.8	5.1			5.2	5
tr	2.4	2.5			2.7	2.5
m1	(UF163524)	(UF163512)	(UF163503)		(UF16989)	(UF18415)
ap	7.0	6.4	6.8		8.6	8.4
tra	2.6	2.4	2.8		3.0	3.2
trp	3.4	3.3	3.2		3.7	4.3
m2	N	M	OR	S	(UF160799)	(UF16991)
ap	4.0	4.63	4.2-4.9	0.3	5.0	5.3
tr	4.0	3.22	3.2-3.3	0.05	3.4	3.5

30-19 Ma. The Arikareean was initially characterized by an assemblage largely collected from the upper Arikaree Group, but including some mammalian genera typical of the lower Arikareean. Tedford et al. (1987) defined the late Arikareean (c.22-18.8 Ma; new dates of MacFadden and Hunt, 1998) by the earliest appearance of *Oligobunus*, *Zodiolestes*, *Daphoenodon*, and *Menoceras*. They also used data collected by researchers on the basal Arikaree formations to define the beginning of the Arikareean. The sparseness of well-dated faunas in the intervening time period did not provide adequate data to establish a detailed biochronology for the greater part of Arikareean time. Woodburne and Swisher (1995) later proposed a division of the Arikareean into four "zones" based on mammal dispersal events: Ar1-Ar2 (30-27.5 Ma), Ar2-Ar3 (27.5-24 Ma), Ar3-Ar4 (24-21 Ma), and Ar4-Hemingfordian (21-19Ma). However, they did not define and characterize these new "zones" and they are not tied to rock units, so biostratigraphic definition is lacking. Later, study of the Whitneyan-Arikareean transition by Tedford et al. (1996) led to a redefined biochronology of the early Arikareean. They proposed that the early Arikareean be defined by the first appearance of *Plesiosminthus* and characterized by the appearances of several autochthonous mammals including *Nanotragulus loomisi*, *Palaeolagus philoi*, and *Palaeocastor nebraskensis*. Furthermore, they suggested that the faunal turnover event at ca. 28 Ma, characterized by the first appearance of *Parvericius*, the eomyid *Pseudotheridomys*, *Promartes*, and the chalicothere *Moropus*, could be used to define the beginning of the medial Arikareean "age." The medial interval, so defined would cover the time from 28 to 22 Ma. To call this "medial Arikareean" would imply an approximate time equivalence to the early and late Arikareean intervals. What is present is a long interval between faunal biochrons at the base of the Arikaree Group and those in the upper part. This long interval is biochronologically undefined and I therefore use "medial" Arikareean Undefined Biochronologic Interval (UBI) for this time period. For purposes of discussion, where other authors have used either the Woodburne and Swisher (1995) chronology or the Tedford et al. (1987) chronology, I have retained the original terms used by those authors.

The most recent discussion of the relationship of the Florida and Gulf Coast Arikareean age sites was by Albright (1998). Based on his faunal analysis, Albright placed Cow House Slough and White Springs in Ar2 (25 and 24.4 Ma, respectively) as the oldest of Florida faunas. Buda, Franklin Phosphate Pit No. 2, and Brooksville 1 were positioned together as slightly younger (Ar2-Ar3: 24-23.5 Ma). SB-1A was correlated with the begin-

ning of Ar3 (22 Ma). The Martin-Anthony oreodont was separated from the fauna (Martin-Anthony LF) found in the clastics above the oreodont and placed as slightly younger than SB-1A at the end of Ar3 (21 Ma). The Martin-Anthony LF itself was placed in Ar4 (19-20 Ma).

Before Albright's correlation of the Florida Arikareean, Morgan (1993) attempted to address the problem of early mammalian biochronology in Florida by studying those sites that placed terrestrial mammals within marine sedimentary contexts, expanding on the work of Tedford and Hunter (1984). He considered Cow House Slough LF and, particularly, the White Springs LF, since the latter was found in nearshore marine units. Within the context of Tedford et al.'s (1987) review of the Arikareean biochron, Morgan correlated both faunas to the early late Arikareean. Morgan (1993) also placed the previously described (MacFadden, 1980) Martin-Anthony LF in the late late Arikareean. This assignment of White Springs LF to the early late Arikareean represented a change from Morgan's (1989) earlier correlation of the marine sediments at White Springs to the upper N4 and lower N5 subtropical foraminiferal zones (22-21 Ma). New evidence in the form of 87Sr/86Sr dating of mollusk shells from the White Springs locality gave an "age" of 24.4 Ma (Jones et al., 1993).

The correlation and age determination of most of Florida's early vertebrate sites present several additional problems. Most of Florida's late Oligocene-early Miocene terrestrial vertebrate fossils are found in karst deposits and thus represent a unique style of sedimentation unlike the Arikareean volcanoclastics that blanket the Great Plains and John Day regions. Lithologic correlation, magnetostratigraphy, and radioisotopic dating frequently can be applied to these western faunas but are often of little use in correlation of the earliest Florida sites. Karst preservation may also introduce another problem in the form of distinct paleoecological biases. Karst depositions may take place on a small scale in any one of a variety of habitats from pine/oak forests to hammocks, swamps, and lakes, and can therefore produce a fauna that is environmentally specific, rather than a broad sampling of taxa. Faunas that appear to be temporally disjunct because of differing taxa may actually be of similar age but come from distinct ecotones. Karst formation creates large open sinkholes, lakes, caves, and solution pipes, which can result in a preserved thanatocoenosis representing only a fraction of the true ecological diversity. Karst features may filter out those animals that are too large to enter the caves, or use of these solution features may be dominated by a particular group of animals that may exclude utilization by other animals.

In view of the above problems, and even consider-

ing the small degree of endemism of the Florida Arikareean taxa identified by Albright (1998), determination of the age of Florida's early "sinkhole" faunas is best done by comparison with the well dated western faunas. This comparison, as well as comparison with Florida localities such as the Hemingfordian Thomas Farm LF, has led to a consensus of Florida sites representing life during the Arikareean NALMA (Frailey, 1978, 1979; MacFadden and Webb, 1982; Tedford et al., 1987; Morgan, 1993; Albright, 1998). However, determination of the relative positions of the Arikareean Florida faunas, and their placement within the subdivisions of the Arikareean has not been universally accepted or adequately constrained.

The Brooksville 2 LF contains some taxa that directly compare with western faunas of the Arikareean. The Brooksville 2 LF includes the hedgehog *Parvericius* whose first appearance is used to define the beginning of Tedford et al.'s (1996) "medial" Arikareean. Entoptychine rodents, represented in the Brooksville 2 LF by an indeterminate genus, also do not appear until the beginning of the "medial" Arikareean (Tedford et al., 1996).

Several taxa present in the fauna serve to constrain the youngest possible date for the fauna. *Centetodon* has its latest occurrence in the McCann Canyon LF of the Great Plains (Korth, 1992), which was placed in the late Arikareean of Tedford et al. (1987). *Agnotocaster* is last recorded in North America at around 27.5 Ma (Xu, 1996). *Nanotragulus* has its last appearance in the late late Arikareean (Ar4). However, Frailey (1979) identified an earlier form, *Nanotragulus loomisi*, as a key element in the Buda LF and compared it directly to the same species in the Arikareean of the Great Plains. *Nanotragulus loomisi* is the holotype species of *Nanotragulus*; a sample of this species from the Arikaree Group of the Muddy Creek region, Hartville Uplift, southeastern Wyoming (including the holotype), averages significantly smaller than individuals of *Nanotragulus* from the upper Arikaree Group of northwest Nebraska (R. M. Hunt, pers. comm., February 1999). Because the species of the genus appear to increase in size through time, *N. loomisi* may be a potentially useful correlator within the Arikareean NALMA. Its presence in the Brooksville 2 LF suggests a pre-late Arikareean age.

Other taxa that compare on the generic level to the Great Plains and also indicate a younger than early Arikareean age for the fauna are *Megalagus abaconis*, *Miohippus* sp., *Herpetotherium* sp., *Enhydrocyon* cf. *pahinsintewakpa*, and *Osbornodon wangi*. Prothero and Emry (1996) listed *Megalagus* as having its last occurrence at the end of the Whitneyan. This range limitation is in error as two Arikareean species have been described,

M. primitivus from the Harrison Formation by Dawson (1967) and *M. dawsoni* from the Fort Logan Formation of Montana by Black (1961). *Megalagus abaconis* is derived in comparison with *Megalagus* from the early Arikareean which have larger buccal roots, less molari-form premolars, and less hypsodont cheek teeth. *Miohippus* sp. from Brooksville 2 LF and Cow House Slough is advanced for the genus and is probably a transitional form between *Miohippus* of the early Arikareean and later *Archaeohippus*. Although *Herpetotherium* is different in dental morphology from the Arikareean *H. youngi* of the Great Plains, it is of similar size and follows the general trend for *Herpetotherium* in size reduction from oldest to youngest species. Also, comparison of this *Herpetotherium* with *Herpetotherium* from the Whitneyan or early Arikareean I-75 LF indicates an ancestor-descendant relationship. The taxonomy and relationships of Florida marsupials will be discussed in Hayes and Wolff, in progress.

The presence of *Osbornodon* in the Brooksville 2 LF is one of the few genera of the Florida Arikareean that ranges into the Hemingfordian. A morphological comparison between the Brooksville 2 LF *Osbornodon wangi* and the Thomas Farm *Osbornodon iamonsensis* shows that the Brooksville 2 LF sample is more plesiomorphic than the Thomas Farm species and thus probably older. In other characters *Osbornodon wangi* is more derived and larger than either *O. sesnoni* or *O. renjieii*, which have their last appearance at the end of the Whitneyan (X. Wang and Tedford, 1996).

Based on the foregoing the new Brooksville 2 LF can be placed in the "medial" Arikareean UBI. The question remains as to where in this very long interval the Brooksville 2 LF fits and where the other Florida Arikareean sites belong in relation to it.

Table 14 is a comparison of the Florida Arikareean faunas and the Arikareean-aged Toledo Bend LF from Texas. Note that all of these faunas have genera and species that are not shared with any of the others, as well as many taxa that are shared by only a few of the other faunas. The importance of the Brooksville 2 LF is that this fauna holds a greater diversity of taxa that link all of the other faunas, thus strengthening their correlation with one another.

Of the Florida Arikareean sites, Brooksville 2 LF has the greatest homotaxial similarity with Cow House Slough and SB-1A. However, only four taxa are shared between all three faunas: *Proheteromys*, *Phlaocyon*, Entoptychinae, and *Nothokemas*. Cow House Slough is the most similar to the Brooksville 2 LF. It has a total of eight taxa that are shared with Brooksville 2 LF. Beside the above, they share *Parvericius*, *Agnotocaster*,

Megalagus, and *Miohippus*. Each of these genera is represented by the same species in both faunas. SB-1A shares seven genera with Brooksville including *Herpetotherium* sp., *Palaeogale minutus*, and *Arikarictis chapini* that are not found in Cow House Slough. The Buda LF contains six of the same genera as Brooksville 2 and two to three of the same species. White Springs LF has four to five of the same genera but none of the same species. Franklin Phosphate Pit No. 2 and the Toledo Bend Local Faunas share *Proheteromys* with Brooksville 2 LF, but only Franklin Phosphate Pit No. 2 LF has *Nothokemas* and only Toledo Bend LF has *Miohippus*.

The Martin-Anthony LF has the least in common with Brooksville 2 or any of the other faunas. I should also note here that the Brooksville 1 LF is not included in this discussion or Table 14 because it consists of only 4 teeth that do not have adequate locality data; Patton (1967) only reported that they originated from somewhere in the Brooksville area.

While it is clear that the Brooksville 2, Cow House Slough, Buda, SB-1A, Franklin Phosphate Pit, and Toledo Bend Local Faunas belong to an interval within the Arikareean age from 28 to 22 Ma, it is more difficult to place these Arikareean faunas in relation to one another considering that the faunal discrepancies between the sites may be merely ecological.

Two taxa are found in almost all Florida Arikareean faunas, *Nothokemas* and *Proheteromys*. Recognition of *Nothokemas* in many of the faunas indicates that this genus is one of the few reliable Arikareean age indicators in Florida. However, at present, it does not separate the Arikareean faunas from each other. (Further study of these samples may indicate evolutionary differences that are reliable for use in correlation.) *Proheteromys* is shared by all Arikareean sites as well as the Thomas Farm locality and analysis of these rodents may determine if there are species level differences that can be used as age indicators. Such a study of *Proheteromys* lay beyond the scope of this study.

The *Phlaocyon* species in these faunas are somewhat enigmatic. Dental characters distinguish *Phlaocyon achoros* at Buda from *P. taylori* in the Brooksville 2 LF. The Brooksville 2 species has more cuspidate molars, but lacks the developed hypocone on the P4 and the developed protostylid on m1 of *P. achoros*. The Thomas Farm *Phlaocyon* has less complex molar teeth but more complex carnassials, suggesting an ancestor-descendant relationship may exist with the Brooksville 2 species that could help determine age. *Phlaocyon* sp. from SB-1A has a developed hypocone on P4 like *P. achoros*, and yet

the SB-1A LF as a whole is much more comparable to Brooksville 2 than to Buda.

The beaver *Agnotocastor* from Brooksville 2, in comparison with the Toledo Bend castorid, *Neatocastor*, is more pleisomorphic. The Toledo Bend and White Springs beaver is taller crowned and the fossettids are more complex. The White Springs beaver also appears to belong to *Neatocastor*, although the material is not diagnostic. In the Great Plains *Agnotocastor* disappears by 27.5 Ma (Xu, 1996). Korth and Emry (1997) propose an ancestor-descendant relationship between *Agnotocastor* and *Neatocastor* that would support an earlier age assignment for Brooksville 2 in relation to Toledo Bend or White Springs.

Entoptychine rodents are found at Cow House Slough and SB-1A as well as Brooksville 2. Rodents are common in the rest of the faunas. The size bias that may reduce the size of larger taxa does not seem to hinder sampling of rodent taxa. Thus the presence of entoptychines may indicate an earlier age for these three faunas.

Rabbits are found in only two other Florida Arikareean faunas, Cow House Slough and White Springs, so their use in correlation is limited. *Megalagus abaconis* is the same taxon as the Cow House Slough lagomorph, but the White Springs rabbit is smaller and more similar to *Archaeolagus*.

In summary, species to species comparison, while not definitive, seems to place Brooksville 2 LF as temporally older than Buda, Franklin Phosphate Pit, White Springs, and Toledo Bend. Brooksville 2 LF, Cow House Slough, and SB-1A are probably close in age, and may represent the "early-medial" Arikareean UBI (28-26 Ma) based on comparisons with Great Plains faunas. This age assignment for the Brooksville 2 LF is also supported by sea level fall during the earlier late Oligocene (Woodburne and Swisher, 1995, Fig.3). Karst formation and exposure of the Florida Platform would have been greatest at this time (28-25 Ma). Buda, Franklin Phosphate Pit No. 2, and Toledo Bend represent a younger time period or the "late-medial" Arikareean UBI. The White Springs LF was numerically dated using Sr87/Sr86 at 24.4 Ma (Jones et al., 1993) and is slightly older than Buda and Toledo Bend. My correlations of the Gulf Coast faunas of Arikareean age agree with that of Albright (1998), with two exceptions. Based on the similarity with the Brooksville 2 LF, SB-1A is moved into an older position, earlier than White Springs (26-25 Ma). Also, Cow House Slough is considered temporally close to the Brooksville 2 LF and therefore correlated to the "early-medial" Arikareean UBI (28-26 Ma).

SUMMARY

The Brooksville 2 Local Fauna contributes a substantial new sample to the growing knowledge of Arikareean mammal faunas in the Gulf Coastal region. It is the most diverse Arikareean fauna now known from Florida, rivaling the Toledo Bend Local Fauna from Texas. The diverse taxa in the fauna aid in correlating many of the Arikareean faunas in Florida and provides for a more precise characterization of the Arikareean NALMA in Florida.

The Brooksville 2 LF formed during the late Oligocene sea level low and at about the time when the Ocala Platform began to arch upward. This led to karst erosion of the early Oligocene Suwannee Limestone. Some terrestrial vertebrates, such as bats and small carnivores, lived and died in these caves and sinkholes. As the karst terrain evolved, other vertebrate remains were transported and redeposited subaqueously in the fissure system form-

ing the five clay pockets (sites 1A-1E) from which the Brooksville 2 LF was recovered.

Faunal correlations place the age of the Brooksville 2 LF within the earlier part of the "medial" Arikareean NALMA UBI (28-26 ma). In Florida, The Brooksville 2 LF shares the most genera and species with the undescribed Cow House Slough LF (eight) followed by the SB-1A LF (seven). These faunas are considered correlative. The Buda LF, Franklin Phosphate Pit No. 2 LF, and Toledo Bend LF are placed together in a later part of the "medial" Arikareean.

Taxa from the Brooksville 2 LF representing first occurrences in Florida include *Agnotocastor*, *Megalagus*, *Enhydrocyon*, and an entoptychine rodent. New species are described for *Megalagus*, *Osbornodon*, and *Phlaocyon*. Two new genera and species of musteloids are described, *Arikarictis chapini* and *Acheronictis webbi*.

The marsupial in the fauna, *Herpetotherium*, may be a new lineage of this genus in the Gulf Coastal Plain. The I-75 *Herpetotherium* is an intermediate species be-

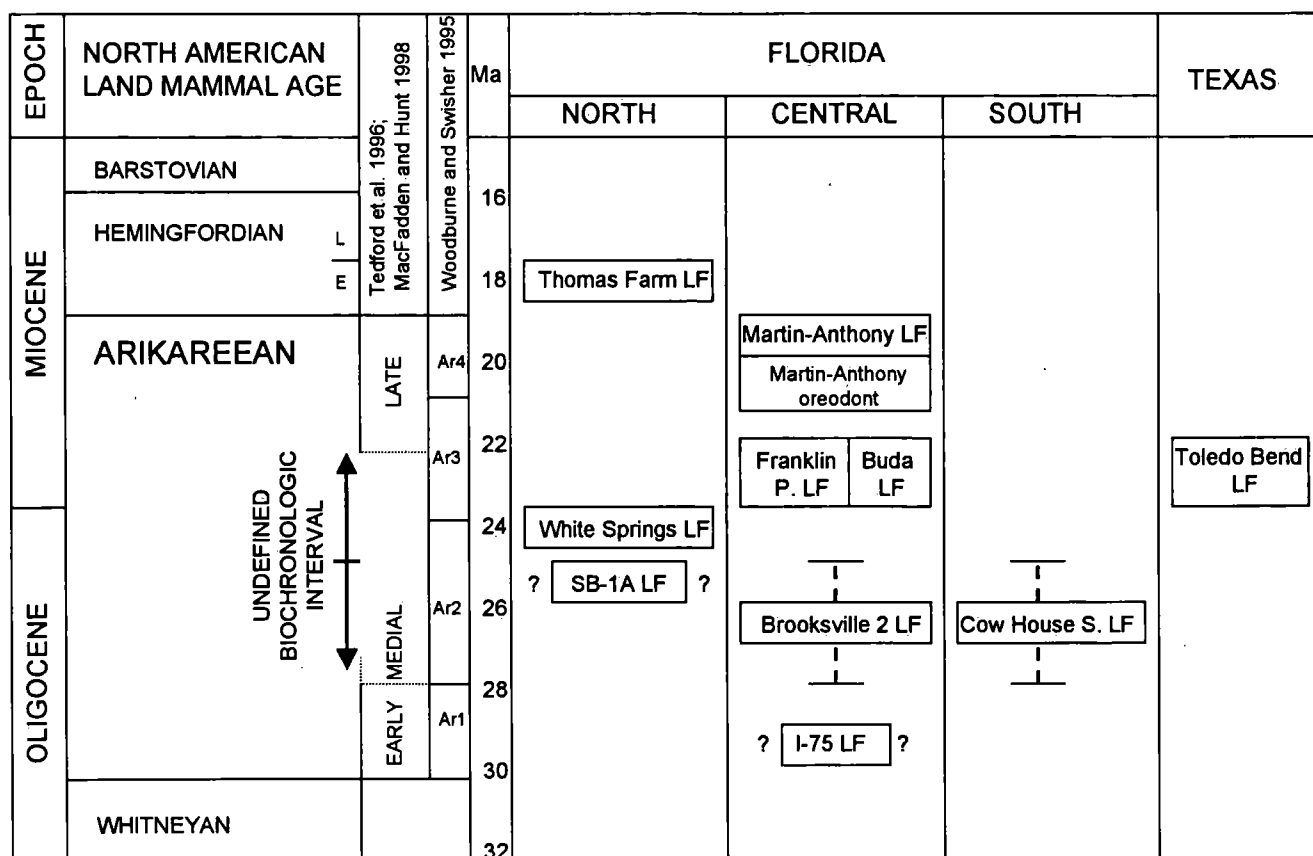


Figure 17. Correlation chart showing age and stratigraphic position of Arikareean and Hemingfordian local faunas of Florida and the Texas Toledo Bend LF. Mammal "ages" and boundaries follows Woodburne and Swisher (1995), Tedford et al. (1996) and MacFadden and Hunt (1998).

tween *H. valens* and *Herpetotherium* n. sp. from Brooksville 2 LF.

Two insectivore taxa, *Centetodon magnus* and the hedgehog *Parvericius*, are well represented in the Brooksville 2 LF for the first time in the Gulf Coastal Region. The described *Ampehechinus* sp. from Buda is here placed in *Parvericius*. *Parvericius* is one of three taxa in the Brooksville 2 LF directly comparable to Great Plains faunas.

Agnotocastor sp. extends the geographic range of this genus into Florida, it is known from the Great Plains and last occurs there in the early Arikareean (27.5MA). The leporid, *Megalagus abaconis*, is an advanced form of this genus, similar to the Arikareean *M. dawsoni* from Montana. Both *Agnotocastor* and *Megalagus* are found in the Cow House Slough LF. The White Spring LF castorid and lagomorph are more derived species, perhaps *Neotocastor* and *Archaeolagus*. After White Springs LF, rabbits and beavers are curiously absent from the Florida record until the Barstovian.

Entoptychine rodents are identified for the first time in Florida. They occur in the Brooksville 2 LF, Cow House Slough, and SB-1A LF. This species is allied to *Gregorymys* and *Entoptychus* from the Great Plains and John Day faunas but is a distinct Gulf Coast species if not genus.

Albright (1996) described *Palaeogale* from the Arikareean of the Gulf Coast on the basis of a single upper carnassial. In light of more conclusive material from Brooksville 2 that can be assigned with confidence to *Palaeogale*, the Toledo Bend specimen is referred to the Mustelidae. The *Palaeogale* material is assigned to *P. minuta* and extends downward the known size-range of this genus.

The two musteloids in the fauna indicate that musteloid diversity within the Arikareean of North America is greater than formerly recognized. They help

fill the gap between the Chadronian *Mustelavus* and the appearance of *Promartes* and *Oligobunis* in the Arikareean. *Acheronictis webbi* is the smallest musteloid in the fauna and may be similar to “*?Plesictis*” sp. described by MacDonald (1970) from the Wounded Knee Fauna. *Arikarictis chapini* is similar in morphology to early European genera of Musteloids.

Phlaocyon is recognized as a common raccoon-sized canid in the Arikareean of Florida. X. Wang et al. (1999) refer Frailey's (1979) “*Bassariscops*” *achoros* from Buda LF to *Phlaocyon*. The sample from Brooksville 2 LF is a new species, *P. taylori*, separate from and smaller than *P. achoros*.

Osbornodon wangi fills part of the time gap between the Whitneyan *O. sesnani* and the Hemingfordian *O. iammonensis*. The presence of *Enhydrocyon* in the fauna marks a first occurrence of this taxon since Tedford and Frailey (1976) referred the Thomas Farm “*Enhydrocyon*” to *Euoplocyon*.

Recognition of *Nothokemas* from almost all the Florida Arikareean faunas makes this wider-ranging taxon important for general correlation of the Florida Arikareean. The smallest artiodactyl in the Brooksville 2 LF, *Nanotragulus loomisi*, is important as one of the species directly comparable to the Great Plains.

The composition of the Brooksville 2 LF reinforces the view that during the Arikareean the faunas of the Gulf Coastal Plain exhibited a high degree of provincialism. The newly described species represent smaller forms of their respective genera, a product of Bergman's rule or an indication of island dwarfing if Florida was still separate from the continent. However, many of the taxa have generic or subfamilial counterparts found in the Great Plains, proving that what Simpson surmised in 1930 is still correct: early Florida shows “Geographic separation (but not isolation) from the Great Plains” (1930:150).

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