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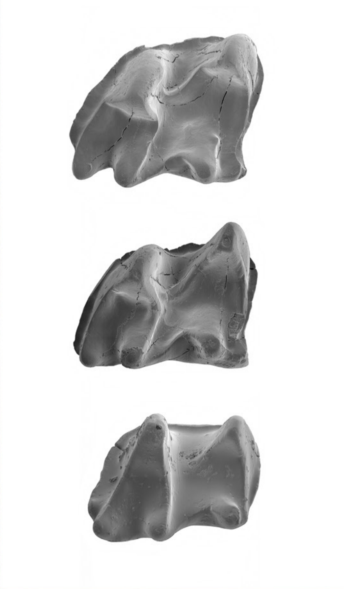

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Cover image: Top row, left, upper molars of *Oligopteryx floridanus*; center, Brooksville 2 Quarry, late Oligocene, Hernando County, Florida; right, lower molars of *Floridopteryx poyeri*. Bottom row, left, Thomas Farm site, early Miocene, Gilchrist County, Florida, left to right, Nicholas Czaplewski, Arthur Poyer, and Gary Morgan; right, *Rhynchonycteris naso* (proboscis bats) hanging under the eaves of a building in Costa Rica.

NEW BATS IN THE TROPICAL FAMILY EMBALLONURIDAE (MAMMALIA: CHIROPTERA) FROM THE OLIGOCENE AND EARLY MIOCENE OF FLORIDA

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ABSTRACT

Three new genera and four new species in the tropical bat family Emballonuridae (Mammalia: Chiroptera) are described from the Oligocene and early Miocene of peninsular Florida. These are: a new genus *Oligopteryx* and two new species, *O. floridanus* and *O. hamaxitos*, from the late Oligocene (early Arikareean) Brooksville 2 Local Fauna in Hernando County, with referred specimens of each species from the early Oligocene (Whitneyan) I-75 Local Fauna in Alachua County; a new genus and species, *Karstopteryx gunnelli*, from the latest Oligocene (late Arikareean) Buda Local Fauna in Alachua County; and a new genus and species, *Floridopteryx poyeri*, from the early Miocene (early Hemingfordian) Thomas Farm Local Fauna in Gilchrist County. Characters that distinguish *Oligopteryx* from other emballonurid genera are: M1 with a much reduced parastylar region and a large talon with a triangular posterolingual extension; M1 and M2 with a prominent hypocone separated from the protocone by a deep, V-shaped notch in the postprotocrista, and deeply concave talon basin; small, single-rooted p3; m1 and m2 with the trigonid narrower and shorter than the talonid, the paraconid and metaconid located close together along the lingual margin, and the entocristid blade-like, V-shaped, and oriented labially. *O. hamaxitos* is distinguished from *O. floridanus* by its smaller size and well-developed paraloph and metaloph on M1 and M2. *Karstopteryx gunnelli* is separated from the two species of *Oligopteryx* by the prominent parastyle, anteriorly oriented preparacrista, and rounded talon. *Floridopteryx* poyeri is characterized by: M1 with a highly reduced parastylar region but with a well-developed parastyle, short preparacrista, small hypocone not separated from the protocone by a notch in the postprotocrista, and a squarish talon; m1/m2 with the talonid much broader than the trigonid, trigonid compressed, shorter than talonid, and with the paraconid and metaconid close together along the lingual margin, large hypoconulid, and anterior root flattened and compressed anteroposteriorly (m1 only). *Oligopteryx* and *Karstopteryx* are considered members of the subfamily Emballonurinae based on the reduced parastylar region of the M1 but are left unassigned at the tribal level. *Oligopteryx* differs from all living emballonurids in the presence of a p3. *Floridopteryx* has a reduced parastylar region on M1 and is also considered an emballonurine, but can be separated from *Oligopteryx* by the presence of a prominent parastyle and lack of a p3. *Floridopteryx* is placed in the monophyletic New World emballonurine tribe Diclidurini. Taphonomy indicates *Oligopteryx* was a colonial cave dweller, whereas *Floridopteryx* more likely roosted in trees, as do most living Neotropical emballonurids. A change from a tropical or subtropical climate in Florida in the Oligocene and early Miocene to a warm temperate climate from the middle Miocene to the present is reflected in the disappearance of emballonurids from Florida after the early Miocene. Molecular studies indicate the Emballonuridae dispersed from Africa to South America in the Oligocene, despite the oldest Western Hemisphere record of this family from the early Oligocene (~30 Ma) of Florida (*Oligopteryx*). We hypothesize emballonurids may have reached North America from Eurasia in the Eocene using an overland route and then dispersed overwater to the then-island continent of South America, with the oldest South American record of that family from the late Oligocene (~25 Ma) of Peru.

RESUMEN

Se describen tres nuevos géneros y cuatro nuevas especies de la familia de murciélagos tropicales Emballonuridae del Oligoceno y el Mioceno temprano de la peninsula del estado de Florida. Estos son: un nuevo género *Oligopteryx* y dos nuevas especies, *O. floridanus* y *O. hamaxitos*, del Oligoceno tardío (edad Arikareense temprano) fauna local Brooksville 2 en el condado de Hernando, con especímenes referidos de cada especie de la fauna local I-75 del Oligoceno temprano (edad Whitneyense) en el condado de Alachua, y un nuevo género y especie, *Karstopteryx gunnelli*, del Oligoceno ultimo (edad Arikareense tardío) de la fauna local Buda en el condado de Alachua; y un nuevo género y especie, *Floridopteryx poyeri*, de la fauna local Thomas Farm del Mioceno temprano (edad Hemingfordiense temprano) en el condado de Gilchrist. Los caracteres que distinguen a *Oligopteryx* de otros géneros embalonúridos son: M1 con una region parastylar muy reducida y un talón de forma triangular con una extension posterolingual; M1 y M2 con un hipocono prominente separado del protocono por una muesca profunda en forma de V y una cuenca en talón profundamente cóncava; p3 pequeño, de raíz única; m1 y m2 con el trigónido más corto que el talónido, el paracónido y el metacónido ubicados muy juntos a lo largo del margen lingual, y el entocrístido en forma de cuchilla, enforma de V y orientado labialmente. *Oligopteryx floridanus* se distingue de *O. hamaxitos* principalmente por su mayor tamaño. *Karstopteryx gunnelli* está separado de las dos especies de *Oligopteryx* por el parastilo prominente, el preparastilo orientado anteriormente, y la talón redondeada. *Floridopteryx* se caracteriza por: M1 con una region parastilar muy reducida pero con un parastilo bien desarollado, preparacrista corto, pequeña hipocono no separado del protocono por una muesca, y un talón cuadrada; m1 / m2 con el talónido mucho más ancho que el trigónido, el trigónido comprimido, más corto que el talónido y con el paracónido y el metacónido muy juntos a lo largo del margen lingual, hipoconulido grande y raíz anterior aplanada y comprimida anterioposteriormente (solo m1). *Oligopteryx* y *Karstopteryx* se consideran miembros de la subfamilia Emballonurinae basada en la region parastilar reducida de M1, pero no se asignan a nivel tribal. *Oligopteryx* difiere de todos los embalonúridos vivos en presencia de un p3. *Floridopteryx* también tiene una region parastilar reducida en M1 y también se considera una Emballonurinae, pero puede separarse de *Oligopteryx* por la presencia de un parastilo prominente y la falta de una p3. *Floridopteryx* se coloca en la tribu Diclidurini monofilética del hemisferio occidental. La tafonomía indica que *Oligopteryx* era un habitante colonial de las cavernas, mientras que *Floridopteryx* probablemente descansaban en los árboles, al igual que la mayoría de los embalonúridos neotropicales vivos. Un cambio de un clima tropical / subtropical en Florida en el Oligoceno y Mioceno temprano a un clima templado cálido desde el Mioceno medio hasta el presente se refleja en la desaparición de los embalonúridos de Florida después del Mioceno temprano. Los estudios moleculares indican que los Emballonuridae se dispersaron desde África hasta América del Sur en el Oligoceno, a pesar del registro más antiguo del hemisferio occidental de esta familia desde el Oligoceno temprano (~30 Ma) de Florida (*Oligopteryx*). Hipotetizamos que los embalónuridos pueden haber llegado a América del Norte desde Eurasia en el Eoceno utilizando una ruta terrestre y luego disperarse sobre el agua hasta el continente de América del Sur, entonces insular, con el registro más antiguo de América del Sur de esa familia desde finales del Oligoceno (~25 Ma) Perú.

Key words: Chiroptera, Emballonuridae, Florida, fossil, Oligocene, Miocene, paleoecology, biogeography, Neotropical

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Morgan, G., S. and N. J. Czaplewski, 2023. New bats in the tropical family Emballonuridae (Mammalia: Chiroptera) from the Oligocene and early Miocene of Florida. Bulletin of the Florida Museum of Natural History 60(3):133–234. https://doi.org/10.58782/flmnh.wefq4531

INTRODUCTION

Much of what we know about the evolutionary history of bats in eastern North America during the middle of the Cenozoic (between about 30 and 18 Ma) is derived from three paleokarst deposits in northern peninsular Florida: the early Oligocene (Whitneyan North American Land Mammal Age–NALMA, ~30 Ma) I-75 Local Fauna (LF), the late Oligocene (early Arikareean NALMA, ~26–28 Ma) Brooksville 2 LF, and the early Miocene (early Hemingfordian NALMA, ~18 Ma) Thomas Farm LF. These three sites document a significant Paleogene-Neogene transition in Florida chiropteran assemblages (Morgan and Czaplewski, 2012), from an Oligocene fauna characterized by families now restricted to the Neotropics (Emballonuridae and Mormoopidae) to an early Miocene fauna that primarily consists of Vespertilionidae but also includes taxa with Neotropical affinities (Emballonuridae, Natalidae, Molossidae). With a few exceptions, most middle Miocene and younger fossil bats from Florida and elsewhere in North America belong to the Vespertilionidae (Czaplewski et al., 2008; Morgan and Czaplewski, 2012), the predominant family in the modern temperate North American chiropteran fauna.

The Emballonuridae, the sheath-tailed or sac-winged bats, occur worldwide in tropical regions, including Mexico, Central America, and South America, as well as Africa, Southeast Asia, Australia, and many Pacific islands (Simmons, 2005). Considering the modern pantropical distribution of emballonurids, it is rather surprising that the oldest fossil record of this group in the New World is from the early Oligocene of peninsular Florida, a region with a warm temperate climate at present that no longer supports members of this family. New World Tertiary records of emballonurids are limited to eight sites, four from Florida, the Oligocene I-75, Brooksville 2, and Buda LFs, and the early Miocene Thomas Farm LF (Morgan and Czaplewski, 2012; this paper), and four localities from South America, the middle Miocene La Venta Fauna from Colombia (Czaplewski, 1997; Czaplewski et al., 2003b) and three sites from Contamana, Peru, a late Oligocene fauna from the Chambira Formation, and early Miocene and late Miocene faunas from the Pebas Formation (Antoine et al., 2016).

Three new genera and four new species of Oligocene and early Miocene emballonurids from Florida are described here and compared to fossil and living emballonurids from the Neotropical Region and the Old World. The paleoecology of the Florida fossil emballonurids indicates a tropical or subtropical climate in the Florida peninsula during the Oligocene, transitioning into a warm temperate climate in the early Miocene. Taphonomy suggests the Florida Oligocene emballonurids were cave-dwelling bats which, together with a previously described extinct genus and species in the family Mormoopidae from the same fossil sites (Morgan et al., 2019), represent the earliest cavernicolous members of the Chiroptera documented in the Western Hemisphere. The single species of Florida Miocene emballonurid was more likely a tree dweller like most modern Neotropical members of the family. Finally, we present a brief review of the pre-Pleistocene fossil record of the Neotropical Chiroptera from South America, as well as fossils from Oligocene and Miocene sites in Florida with Neotropical affinities.

METHODS AND MATERIALS

Chiropteran dental terminology follows Czaplewski et al. (2008) and Ravel et al. (2016). The abbreviations for teeth in mammals are standard, with upper case letters for upper teeth and lower case letters for lower teeth: I/i (upper/lower incisors), C/c (upper/lower canines), P/p (upper/lower premolars), and M/m (upper/lower molars). Tooth positions are identified by numbers. For example, P4 is an upper fourth premolar and m3 is a lower third molar. The identity of the anteriormost lower premolar in bats that possess three lower premolars, such as *Oligopteryx*, is controversial. Most authors have followed Miller (1907) in considering p1 as the missing lower premolar in bats, with the remaining premolars being p2, p3, and p4. However, Thomas (1908), Simmons and Conway (2001), and Giannini and Simmons (2007) regarded the first lower premolar as the p1 and considered the p2 to be the missing lower premolar in the Chiroptera. We follow Miller (1907), Hand et al. (2015), and Cirranello et al. (2016) in recognizing the three lower premolars in bats as p2, p3, p4, with p1 missing. In describing a petrosal, we use the terminology of Staněk (1933), Henson (1970), Simmons and Geisler (1998), and Giannini et al. (2006). The terminology for chiropteran postcranial elements follows Vaughan (1959), Smith (1972), Czaplewski et al. (2008), and Gaudioso et al. (2020). We estimated body mass in grams of the extinct taxa of emballonurid bats using equations generated by (Gunnell et al., 2009). All other measurements are in mm.

We compared the I-75, Brooksville 2, Buda, and Thomas Farm emballonurid fossils to teeth, dentaries, and postcranial skeletons of at least one species in each of the 14 genera of extant Emballonuridae (list of modern comparative material examined in Appendix 1). We also compared the Florida Cenozoic emballonurids to five extinct genera of emballonurids from Europe and Africa, *Afrillonura*, *Dhofarella*, *Pseudovespertiliavus*, *Tachypteron*, and *Vespertiliavus*, primarily from the literature. Most of our morphological comparisons of the Florida fossil emballonurids are at the generic level.

All Tertiary sites from Florida that have produced bats were collected using standard screenwashing techniques for microvertebrates. Before the mid 1970s, screens finer than standard window screen (16 mesh, 1.5 mm opening) were not in general use, and thus isolated teeth of small bats may have been lost from sites screenwashed during this time period (e.g., I-75, Buda, early Thomas Farm collections). All Florida sites collected from the early 1980s to the present, including later Thomas Farm collections and Brooksville 2, were screenwashed through both standard window screen and fine mesh brass screen (24 mesh, 1.0 mm opening). After 1980, no identifable bat specimens were lost from Florida Tertiary sites during the screenwashing process.

The I-75, Brooksville 2, Buda, and Thomas Farm emballonurid fossil specimens are from the vertebrate paleontology collection of the Florida Museum of Natural History, University of Florida, Gainesville (UF). Modern comparative skeletons of Emballonuridae are from the mammal collections of the American Museum of Natural History, New York (AMNH); Museum of Southwestern Biology, Department of Biology, University of New Mexico, Albuquerque (MSB); Oklahoma Museum of Natural History, University of Oklahoma, Norman (OMNH); Florida Museum of Natural History, University of Florida (UF-M); and U. S. National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Other abbreviations are: LF (Local Fauna); Ma (Mega-annum or millions of years); MNI (minimum number of individuals); NISP (number of identifiable specimens); NALMA (North American land mammal age); SALMA (South American land mammal age).

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), and hence the new genus and species names contained herein are available under that Code. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank Publication number for this issue is: D72FD99C-656E-4FF5-9813-2F1C71A53B9.

GEOLOGIC SETTING AND CHRONOLOGY

Prior to the Oligocene, the region that is now the Florida peninsula was entirely submerged, consisting of shallow tropical reefs and carbonate banks. Consequently, much of northern peninsular Florida is now underlain by Eocene and Oligocene marine limestones. Sometime in the latter part of the early Oligocene (Rupelian) about 30 million years ago (Ma), Florida first emerged above sea level based on the presence of the I-75 land vertebrate fauna correlated with the Whitneyan NALMA (30–32 Ma). Throughout the remainder of the Cenozoic, the Florida peninsula fluctuated between submerged and emergent, depending upon changes in relative sea level. During this time period, the highly soluble Paleogene limestones of northern Florida were acted upon by both chemical and physical erosional processes to develop one of the most extensive karst terrains in North America (Lane, 1986; Florea, 2008). From a paleontological standpoint, the most significant aspect of the north Florida karst geomorphic province is the abundance of terrestrial vertebrate deposits occurring in current or former caves, fissures, sinkholes, and other paleokarst features (Morgan and Hulbert, 2008). The limestones in northern Florida are mined commercially, which has resulted in the discovery of most of the fossil deposits. More than 150 vertebrate fossil sites of karst origin are known from the Florida peninsula, including many deposits that contain bats (Morgan and Hulbert, 2008; Morgan and Czaplewski, 2012). Nowhere else in North America are karst-derived vertebrate fossil deposits of Cenozoic age found in such abundance. Florida vertebrate faunas of karst origin range in age from the Oligocene through the Pleistocene, with the oldest being the early Oligocene I-75 LF and the largest concentration of sites from the late Pleistocene (Rancholabrean NALMA).

The common occurrence of bat fossils in karst deposits from northern peninsular Florida strongly indicates that many of these sites represent the remnants of former cave systems. The richest pre-Pleistocene bat faunas from Florida (I-75, Brooksville 2, Thomas Farm) were derived from sediment-filled fissures or sinkholes in Paleogene limestones. In addition to bats, these karst deposits often contain large samples of small, non-volant mammals such as marsupials, lipotyphlans (‘insectivores’), rodents, and lagomorphs, as well as other small vertebrates, including frogs, toads, salamanders, lizards, snakes, and birds. Despite their original deposition in caves, pre-Pleistocene karst faunas in Florida do not occur in what are currently caves. The same physical and chemical erosional processes that originally formed the caves eventually destroyed them. With the collapse of the caves, their contained sediments became buried, and the caves were no longer accessible from surface entrances. We suspect that only a small percentage of these buried karst deposits have been uncovered within the past century or so by limestone mining operations, as heavy equipment exposed deeply buried clay and sand deposits containing fossils. This process of cave formation and destruction appears to have occurred fairly rapidly in a geologic sense, because all vertebrate fossils so far recovered from surficial deposits in Florida caves are late Pleistocene (Rancholabrean) in age. There are numerous karst-derived vertebrate faunas of early to middle Pleistocene age (Blancan and Irvingtonian NALMAs) from peninsular Florida, all of which are from previously buried cave or sinkhole deposits (Morgan and Hulbert, 2008).

Because Florida karst deposits usually consist of isolated pockets of sediment that cannot be directly correlated stratigraphically, their significance for biochronology has often been overlooked or downplayed. However, the abundance in many Florida sites of small mammals and age-diagnostic large mammals, including carnivores, horses, and artiodactyls, often allows precise biochronologic comparisons with faunas of similar age in western North America that have associated geochronological data such as radioisotopic dates or geomagnetic polarity stratigraphy (e.g., Frailey, 1978, 1979; Pratt and Morgan, 1989; Morgan, 1993; Albright, 1998; Hayes, 2000, 2005; MacFadden and Morgan, 2003; Tedford et al., 2004; Albright et al., 2008; Morgan and Hulbert, 2008; Czaplewski and Morgan, 2015). Moreover, Florida faunas are often more diverse and have larger and better-preserved fossil samples than faunas of equivalent age in western North America. Most Florida Cenozoic vertebrate assemblages are ‘local faunas’ in the sense of Tedford (1970), with the following definition from Woodburne (2004, xiii): “Local Fauna: An aggregate of fossil vertebrate species that have a limited distribution in time from a number of closely grouped localities in a limited geographic area…A local fauna could be based on taxa from a single locality.” Indeed, most local faunas from Florida have been described based on the vertebrate fossils from a single locality, including I-75 and Thomas Farm (Patton, 1969a; Pratt, 1989, 1990). Brooksville 2 and Buda are derived from several separate karst sediment pockets in a limited geographic area, specifically a limestone quarry (Frailey, 1979; Hayes, 2000). Since Florida Cenozoic local faunas mostly occur in a single locality and in a narrow stratigraphic interval, there are minimal complications from ecological mixing and time averaging. Vertebrate local faunas or faunas from western North America often occur over a considerably larger geographic area and through a substantial stratigraphic interval and, as such, time averaging and ecological mixing can become substantial error factors in evaluating the biochronology and/or paleoecology of these sites.

Our biochronology follows the North American land mammal ages (NALMA), which are biochronologic units based on mammalian evolution in North America, specifically an association of fossil mammals that represents a particular interval of geologic time. Most NALMA are defined based on a specific association of mammalian genera. For the faunal definitions and age of the NALMAs represented in Florida Tertiary paleokarst deposits that contain emballonurid bats, we follow Prothero and Emry (2004) for the Whitneyan NALMA (early Oligocene) and Tedford et al. (2004) for the Arikareean and Hemingfordian NALMAs (late Oligocene and early Miocene). We also incorporate the updated Arikareean biostratigraphy of Albright et al. (2008).

FLORIDA FOSSIL SITES CONTAINING EMBALLONURIDAE

I-75

The I-75 Local Fauna (LF) was discovered in 1965 during the construction of Interstate Highway 75 (‘I-75’) through the southwestern edge of Gainesville, Alachua County, in northern peninsular Florida (Fig. 1). The site was located in a roadcut at the southwest corner of the intersection of I-75 and Florida State Route 121 but was destroyed by road building activities shortly after its discovery. Mervin Kontrovitz of the University of Florida initially discovered the I-75 site, which was collected by Florida State Museum (now Florida Museum of Natural History) field crews. The fossiliferous sediments in the I-75 site consisted of massive, slightly sandy, dark brown to black clays, deposited in a small karst solution feature 5 m in diameter and 2 m deep, developed in Eocene marine limestone (Patton, 1969a).

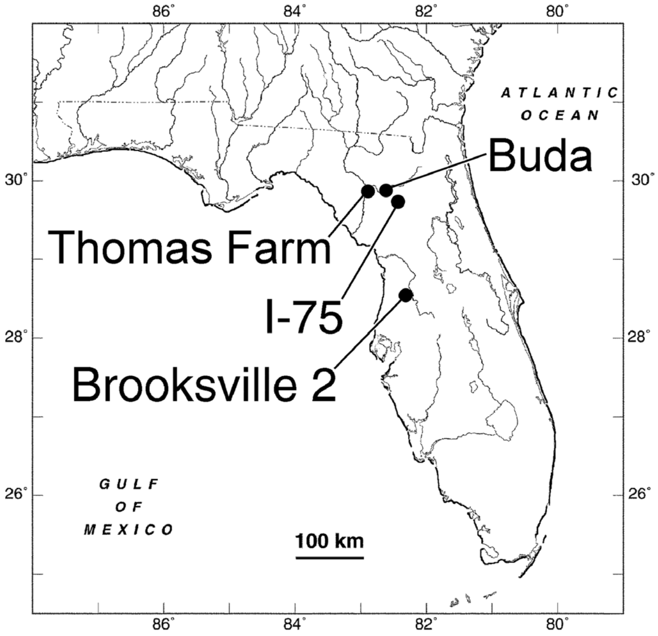

Figure 1. Outline map of the southeastern United States showing Florida, with locations of Oligocene (I-75, Brooksville 2, and Buda) and Miocene (Thomas Farm) sites containing fossils of Emballonuridae.

Considering the small size of the fossiliferous deposit, the I-75 site has a diverse vertebrate fauna composed of about 45 species. Patton (1969a) published a preliminary vertebrate faunal list and Holman (1999) and Holman and Harrison (2000, 2001) described the snake fauna. Hayes (2000) updated the mammalian faunal list from Patton (1969a). The herpetofauna includes anurans (both bufonids and scaphiopodids), an indeterminate sirenid salamander, a small land tortoise, a pond turtle, the lizard *Peltosaurus*, and an impressive snake fauna consisting of nine species of boids and colubrids (Holman, 1999; Holman and Harrison, 2000, 2001). Inexplicably, birds are absent from the I-75 LF. The fauna of large mammals consists of (from Patton, 1969a; Hayes, 2000): two species of carnivorans, the amphicyonid *Daphoenus* and the small mustelid *Palaeogale*; the equid *Miohippus* sp.; a tayassuid; two oreodonts; and the small leptomerycid artiodactyl *Leptomeryx* sp., the most abundant mammal in the fauna. Small mammals include: the marsupial *Herpetotherium* cf. *merriami* (Hayes, 2005), the large lipotyphlan *Centetodon* cf. *wolffi*; the lagomorph *Palaeolagus* sp.; four species of rodents, *Eutypomys* sp., a heteromyid, and two eomyids; as well as seven species of bats (described in more detail below).

Marine vertebrates also were recovered from I-75, including sharks, rays, and bony fish (Patton, 1969a; Tessman, 1969). Because of the association of marine, freshwater, and terrestrial taxa, Patton (1969a) suggested there may have been some reworking of the I-75 deposit. In most other Florida Tertiary sites containing a mixture of marine and nonmarine vertebrates, the marine vertebrates far outnumber the terrestrial component of the fauna, and most teeth of small mammals are isolated and show some evidence of transport and water wear (Morgan, 1993). However, terrestrial vertebrates dominate the I-75 fauna and there are several partial mandibles and maxillae with teeth representing bats and other small mammals. Furthermore, most of the isolated teeth and limb bones are well preserved and show little evidence of water wear. The most plausible explanation would seem to be that the terrestrial vertebrates from the I-75 site were deposited subaerially in a small cave or fissure. Shortly thereafter, with a rise in sea level the marine vertebrates were deposited, with minor reworking. Florida had only recently emerged above sea level in the late early Oligocene and probably consisted of a short, narrow peninsula of low relief. A slight rise in sea level would have been sufficient to inundate most of the land present in Florida at that time, including the cave/fissure represented by the I-75 site.

I-75 is the oldest land vertebrate fauna known from Florida, referred to the Whitneyan NALMA by Patton (1969a) and most subsequent workers (Savage and Russell, 1983; Emry et al., 1987; Prothero and Emry, 2004). The Whitneyan represents a restricted interval of time in the early Oligocene (~30-32 Ma), known primarily by faunas from the Northern Great Plains in Nebraska, South Dakota, and Wyoming. The following is a brief discussion of the most biochronologically diagnostic land mammals present in the I-75 LF. Four isolated teeth of a brachydont horse from I-75 are identified as *Miohippus* sp., although Patton (1969a) referred these teeth to *Mesohippus*. These teeth compare more closely with *Miohippus* than *Mesohippus* on the basis of the characters discussed by Prothero and Shubin (1989), including larger size and well-developed hypostyles on the upper molars. *Miohippus* occurs from the Chadronian through the early Arikareean but is most typical of Whitneyan and Arikareean faunas (Emry et al., 1987; Prothero and Shubin, 1989). The I-75 *Miohippus* teeth appear to be most similar in size and morphology to *M. intermedius* from the late Whitneyan of South Dakota. A large sample of isolated teeth is tentatively referred to the small leptomerycid artiodactyl *Leptomeryx*, although Patton (1969a) and Hayes (2005) referred these teeth to *Nanotragulus*. *Leptomeryx* occurs from the Chadronian through the early Arikareean, whereas *Nanotragulus* first appears in the early Arikareean (Prothero and Emry, 2004; Tedford et al., 2004).

The geolabidid lipotyphlan *Centetodon* is represented in the I-75 LF by a partial upper molar and three complete lower molars. The morphology and size of the I-75 *Centetodon* teeth are similar to *C. wolffi* from the Orellan and Whitneyan of South Dakota, the largest species in the genus (Lillegraven et al., 1981). Hayes (2005) identified two upper molars from I-75 as the marsupial *Herpetotherium* cf. *merriami*, originally described from the early Arikareean John Day Formation of Oregon. A single upper cheektooth of a small leporid is tentatively referred to *Palaeolagus*, the most common rabbit in Orellan and Whitneyan faunas. *Palaeolagus* went extinct in the early Arikareean. The large beaver-like rodent *Eutypomys* is represented by about 20 teeth from the I-75 fauna. *Eutypomys* is typical of Whitneyan and Orellan faunas in the Great Plains, but survived into the early Arikareean (Macdonald, 1963, 1970; Tedford et al., 1996; Prothero and Emry, 2004).

The presence of *Centetodon*, *Palaeolagus*, *Eutypomys Miohippus*, and *Leptomeryx* establishes an age of early late Arikareean or older (older than 24 Ma) for the I-75 LF, as none of these genera are known to survive into the latest Arikareean (Ar4; Lillegraven et al., 1981; Tedford et al., 1996, 2004; Albright et al., 2008). All five of these genera also occur in both the Orellan and Whitneyan NALMAs. A post-Orellan age is suggested by the presence of an advanced species of *Miohippus* near *M. intermedius*, and an age no younger than Whitneyan is indicated by the occurence of *Centetodon wolffi*. The absence of mammals clearly indicative of the Arikareean (e.g., *Nanotragulus*) favors a Whitneyan age, probably late Whitneyan (~30-31 Ma; Prothero and Emry, 2004; Albright et al., 2008), which is several million years older than the late early Arikareean (Ar2; ~26-28 Ma) Brooksville 2 LF. The similarity of bats from I-75 and Brooksville 2 suggests these two faunas are fairly close in age. Although their chiropteran faunas are similar, the remainder of the mammalian assemblages from these two sites have few genera and no species in common (Hayes, 2000).

I-75 provides one of the earliest records of the taxonomic diversity and community structure of North American Late Paleogene chiropteran faunas. About 40 specimens representing seven species of bats are known from I-75, including: *Oligopteryx floridanus* and *O. hamaxitos* (described in this paper), the oldest members of the Emballonuridae in the New World; *Koopmanycteris palaeomormoops*, the oldest known member of the Mormoopidae (Morgan et al., 2019); *Speonycteris aurantiadens* and *S. naturalis* (type locality) in the extinct noctilionoid family Speonycteridae (Czaplewski and Morgan, 2012); an indeterminate genus and species representing the oldest known member of the Natalidae (Morgan and Czaplewski, 2003); and a large indeterminate genus and species of Vespertilionidae (Morgan and Czaplewski, 2012). The most abundant bats in the I-75 fauna are *Oligopteryx floridanus* and *Koopmanycteris palaeomormoops*.

BROOKSVILLE 2

The Brooksville 2 site was discovered in 1994 in an abandoned limerock quarry of the Florida Rock Industries company, about 8 km northwest of Brooksville, Hernando County, central Florida (Fig. 1). Brooksville 2 consists of clays and sands filling five small karst solution features in the marine lower Oligocene Suwannee Limestone (Hayes, 2000). See field photos of the Brooksville 2 Quarry in Figure 2. FLMNH crews visited the Brooksville Quarry on numerous field trips between April 1994 and February 1995. Although some specimens of larger vertebrates were found on the surface, the fossils were collected primarily by screenwashing because of the abundance of microvertebrates. Approximately 500 kg of sediments were screenwashed from solution features in the quarry in which the Brooksville 2 site was located (Hayes, 2000).

The vertebrate assemblage from Brooksville 2 is composed predominantly of small terrestrial vertebrates, including frogs, lizards, snakes, and a diverse fauna of small mammals, but no birds. Mead (2013) reported three vertebrae of a tiny scolecophidian snake from Brooksville 2. Larger mammals are represented primarily by isolated teeth. Hayes (2000) reported 27 species of mammals from Brooksville 2. He described the lipotyphlans, carnivorans, lagomorphs, and selected taxa of rodents, and briefly reviewed the ungulates. Hayes (2005) identified the marsupial *Herpetotherium fugax* from Brooksville 2. The large sample of bats is described in more detail below. The ungulates and carnivorans include (Hayes, 2000): the horse *Miohippus*; a phenacocoeline oreodont; the camel *Nothokemas waldropi*; the tiny artiodactyl *Nanotragulus loomisi*; and six species of carnivorans, *Palaeogale minuta*, the musteloids *Acheronictis webbi* (type locality) and *Arikarictis chapini* (type locality), and the canids *Enhydrocyon* cf. *pahinsintewakpa*, *Osbornodon wangi* (type locality), and *Phlaocyon taylori* (type locality). In addition to the small didelphid marsupial *Herpetotherium fugax* and five species of bats, the small mammal fauna also includes: two lipotyphlans, the geolabidid *Centetodon magnus* and the erinaceid *Parvericius montanus*; the lagomorph *Megalagus abaconis* (type locality); and numerous rodents, including sciurids, eomyids, two heteromyids, the castorid *Agnotocastor* sp., and an undescribed entoptychine geomyoid (Hayes, 2000, 2005; this paper).

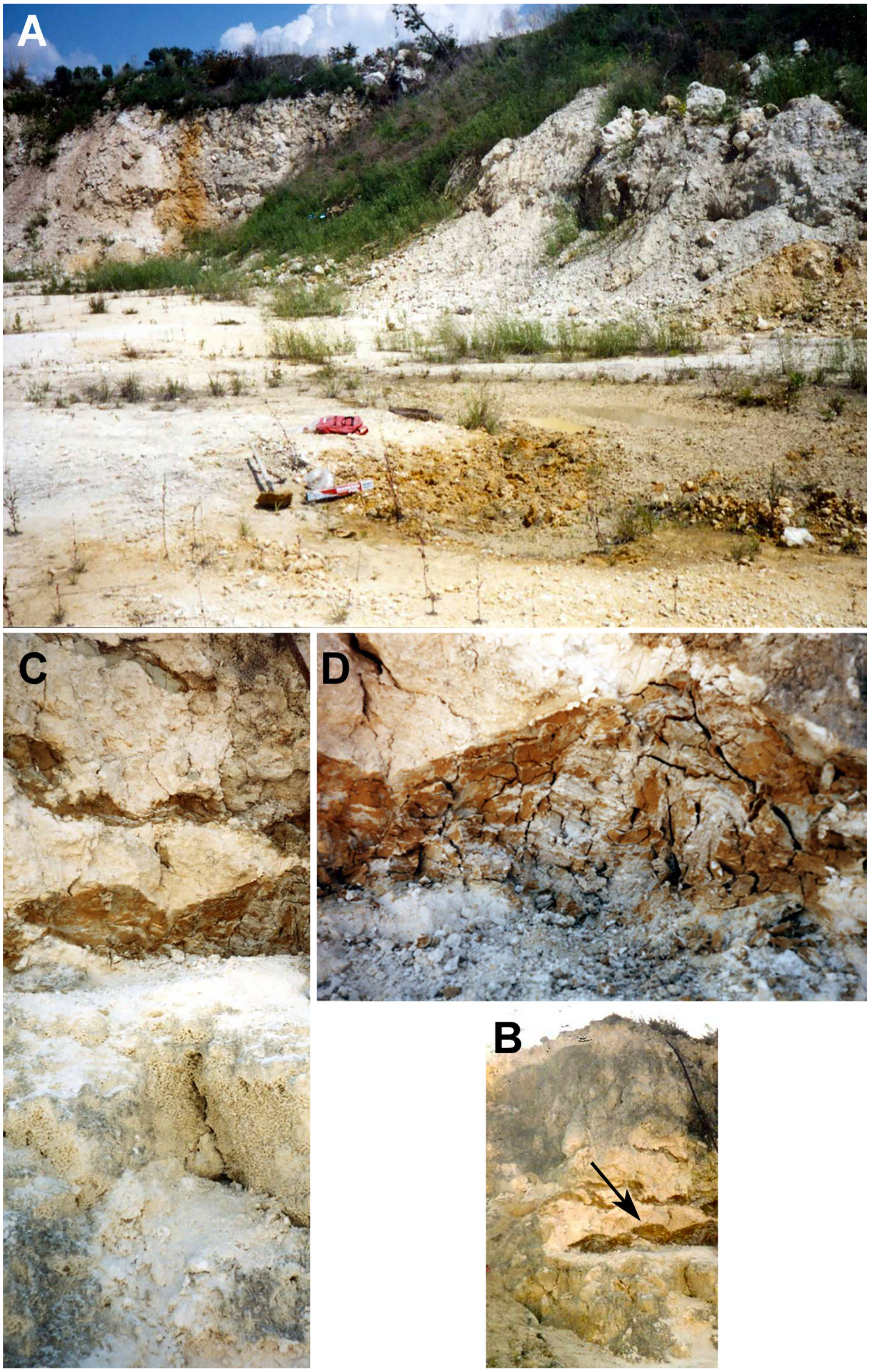

Figure 2. Field photographs of the late Oligocene (early Arikareean) Brooksville 2 site (as it appeared in the mid 1990s), located in an abandoned limerock mine northwest of Brooksville, Hernando County, Florida. The Brooksville 2 Local Fauna is the type locality of the emballonurid bats *Oligopteryx floridanus* and *O. hamaxitos*. A. Overview of the Brooksville Quarry showing exposures of the marine lower Oligocene Suwannee Limestone. B. View of the quarry wall showing a karst deposit (indicated by black arrow), within the Suwannee Limestone. C. Close-up view of the same karst deposit shown in B. D. Even closer view of the same karst deposit in B and C, showing the fossiliferous laminated red and gray clays and fine sands (photos courtesy of Glynn Hayes).

Hayes (2000) determined the age of the Brooksville 2 LF through biochronologic comparisons with other faunas from Florida and the Gulf Coast representing the Arikareean NALMA (Albright, 1998), and with Arikareean faunas from western North America. Preservation of the Brooksville 2 fossils in isolated karst solution features precludes direct stratigraphic correlation with described Oligocene and Miocene stratigraphic units from northern Florida. We follow Albright et al. (2008) for the updated calibration and subdivisions of the Arikareean NALMA. The maximum age of Brooksville 2 is constrained by the presence of the erinaceid *Parvericius* and entoptychine rodents, both of which appear at the beginning of the late early Arikareean (Ar2, ~28 Ma; Tedford et al., 1996, 2004; Albright et al., 2008). The minimum age of the site is restricted to early late Arikareean (Ar3) by the occurrence of *Miohippus*. Albright et al. (2008) recorded the range of *Miohippus* as extending into the early late Arikareean in the John Formation of Oregon, disappearing at about 24 Ma. Hayes (2000) placed the Brooksville 2 LF in the 'medial' Arikareean (late Oligocene; between 24 and 28 Ma). With more recent changes in the boundaries of the subdivisions within the Arikareean (Albright et al., 2008), the age range Hayes (2000) suggested for Brooksville 2 would now place this fauna in either the late early Arikareean (Ar2) or the early late Arikareean (Ar3). The co-occurrence of *Parvericius* and entoptychine rodents with *Miohippus*, together with the strong similarity between the chiropteran faunas from Brooksville 2 and the Whitneyan I-75 LF, supports a late early Arikareean age (~26-28 Ma) for the Brooksville 2 LF. An analysis of the mammalian biochronology of Brooksville 2 at the species level, rather than the generic level, would probably yield a more precise age for this fauna.

The chiropteran sample from Brooksville 2 consists of about 200 fossils representing five species: the emballonurids *Oligopteryx floridanus* and *O. hamaxitos* (both described in this paper), with Brooksville 2 as the type locality for both species; the mormoopid *Koopmanycteris palaeomormoops* (type locality); *Speonycteris aurantiadens* (type locality) in the extinct family Speonycteridae; and an indeterminate genus and species of molossid (Czaplewski et al., 2003a; Czaplewski and Morgan, 2012; Morgan and Czaplewski, 2012; Morgan et al., 2019). With the exception of the molossid, all of these species are shared with I-75. Brooksville 2 has the second largest bat sample from any Florida Tertiary site, after Thomas Farm, and the third most diverse bat fauna after Thomas Farm and I-75. As with the I-75 LF, the most common bats from Brooksville 2 are two species from families currently restricted to the tropics, the emballonurid *Oligopteryx floridanus* and the mormoopid *Koopmanycteris palaeomormoops*.

It seems rather remarkable that the chiropteran fauna from Brooksville 2 shares four of its five species with I-75, *Koopmanycteris palaeomormoops*, *Oligopteryx floridanus*, *O. hamaxitos*, and *Speonycteris aurantiadens*, whereas the non-volant mammalian faunas from these two sites have no species in common and share only three genera (*Centetodon*, *Herpetotherium*, and *Miohippus*). Both the Brooksville 2 and I-75 sites are fissure deposits in which the fossils were originally deposited in caves, which is supported by the abundance of cave-dwelling bats, including the two species of Emballonuridae described here, *Oligopteryx floridanus* and *O. hamaxitos*, and a previously described member of the Mormoopidae, *Koopmanycteris palaeomormoops* (Morgan et al., 2019). The similar chiropteran faunas in these two sites primarily consist of species with tropical affinities (Emballonuridae, Mormoopidae), indicating Florida had a tropical/subtropical climate during their deposition. Apparently, the chiropteran fauna was well-adapted to the climate of peninsular Florida in the Oligocene and underwent only minimal evolutionary change over a period of several million years. The total lack of overlap at the species level between the non-volant mammalian faunas from Brooksville 2 and I-75 is indicative of both evolutionary changes within genera (e.g., *Centetodon*, *Herpetotherium*, and *Miohippus*) and overall faunal change associated with the age difference between Whitneyan and early Arikareean faunas (e.g., the small ruminant *Leptomeryx* and eutypomyine rodents in I-75 compared to the tiny ruminant *Nanotragulus*, entoptychine rodents, and erinaceid *Parvericius* in Brooksville 2). The differences between the non-volant mammalian faunas in these two sites appear to be primarily related to their difference in age, with I-75 about 2 million years older.

BUDA

The Buda Quarry is an abandoned limestone mine located about 8 km southwest of High Springs, Alachua County, northern peninsular Florida (Fig. 1). The fossiliferous deposit, long since destroyed by mining operations, consisted of three shallow, clay-filled fissures from 1 to 3 m in diameter that probably shared a common opening, eroded into Eocene marine limestone. Frailey (1979) reported 12 taxa of large mammals from the Buda LF: five carnivorans, the amphicyonid *Daphoenodon notionastes*, the canids *Bassariscops achoros* and *Cynarctoides* sp., a mustelid, and a nimravid; two perissodactyls, the small chalicothere *Moropus* sp. and an indeterminate equid; and five artiodactyls, a small tayassuid, a phenacocoeline oreodont, two camelids, and the tiny ruminant *Nanotragulus loomisi*, the most abundant mammal in the fauna. Wang et al. (1999) restudied the Buda canid fauna, transferring *Bassariscops achoros* to the genus *Phlaocyon*, referring *Cynarctoides* to the species *C. lemur*, and identifying the species *Cormocyon* cf. *copei.* The Buda LF also has a significant small mammal fauna that remains mostly unstudied. Rich and Patton (1975) reported the erinaceid *Amphechinus* from Buda, later reidentified as *Parvericius* by Hayes (2000). Czaplewski and Morgan (2015) described the last surviving apatemyid (Apatotheria) *Sinclairella simplicidens* from Buda. Other small mammals include the geolabidid lipotyphlan *Centetodon* cf. *magnus*, and three rodents, the jimomyid *Texomys* sp., the eomyid *Arikareeomys* sp., and a heteromyid, as well as the emballonurid bat *Karstopteryx gunnelli* described here (Hayes, 2000; Czaplewski and Morgan, 2015).

Frailey (1979) regarded the Buda LF as late Arikareean, and Albright (1998) and Hayes (2000) placed this fauna in the early late Arikareean (Ar3). The most compelling evidence for a late Arikareean age is the presence of the amphicyonid *Daphoenodon*, one of the defining genera for the late Arikareean, and the small chalicothere *Moropus* cf. *oregonensis* (Coombs et al., 2001; Tedford et al., 2004). According to Albright et al. (2008), *Daphoenodon* and *Moropus* first appeared in the John Day Formation in Oregon in the early late Arikareean at about 25 Ma (early Ar3). However, several other mammals from Buda are more typical of early Arikareean faunas (Ar1 and/or Ar2), including *Cynarctoides lemur* and *Cormocyon* cf. *copei* (Wang et al., 1999; Albright et al., 2008). Two small mammal genera, *Centetodon* and *Arikareeomys*, are also more typical of the early Arikareean but occur in the early late Arikareean. We follow Albright (1998), Hayes (2000), and Czaplewski and Morgan (2015) in placing the Buda LF in the early late Arikareean (early Ar3; ~24-26 Ma; latest Oligocene), based on the co-occurrence of *Daphoenodon* and *Moropus* that first appear in the Ar3, together with *Centetodon* and *Arikareeomys* that last occur in the Ar3.

The Buda LF chiropteran fauna consists of a single tooth (M1), described below as a new genus and species, *Karstopteryx gunnelli*. We suspect the sparse bat sample from Buda may be due to a collecting bias, because only minimal screenwashing for microvertebrates was conducted at this site and nothing finer than window screen (1.5 mm opening) was used. Dental differences between *Karstopteryx* and the two species of *Oligopteryx* from the somewhat older Brooksville 2 LF confirm that significant morphological changes occurred in the Florida emballonurid lineage in the late Oligocene, supporting the younger early late Arikareean age of the Buda LF proposed by other authors (Frailey 1979; Hayes, 2000; Czaplewski and Morgan, 2015).

THOMAS FARM

The Thomas Farm site is located 12 km north of Bell in Gilchrist County, northern peninsular Florida (Fig. 1). Thomas Farm has produced the best known and most diverse early Miocene (early Hemingfordian NALMA; He1) vertebrate fauna in eastern North America. The site consists of clays and sands filling a sinkhole developed in Eocene marine limestone. See field photos of the Thomas Farm site in Figure 3. Pratt (1989, 1990) concluded that Thomas Farm consisted of a 30 m deep, vertical-walled sinkhole surrounded by a forested habitat. There is a large sample of bat fossils in a 1 m thick lime sand near the top of the section that is also rich in other small vertebrates. Most of the small vertebrates appear to have been deposited in a former cave system developed in the wall of the sinkhole, either as a coprocoenosis derived from the scat of small mammalian carnivores or the pellets of raptorial birds, or through the natural accumulation of carcasses on a cave floor in the case of the bats (Pratt, 1989).

The Thomas Farm LF consists of more than 90 species of vertebrates (Webb, 1981; Pratt, 1989, 1990), primarily composed of terrestrial forms but also including a freshwater component of frogs, salamanders, pond turtles, alligators, and aquatic birds. Thomas Farm has 23 species of large mammals, the most abundant of which is the horse *Parahippus leonensis* (Hulbert, 1984), and

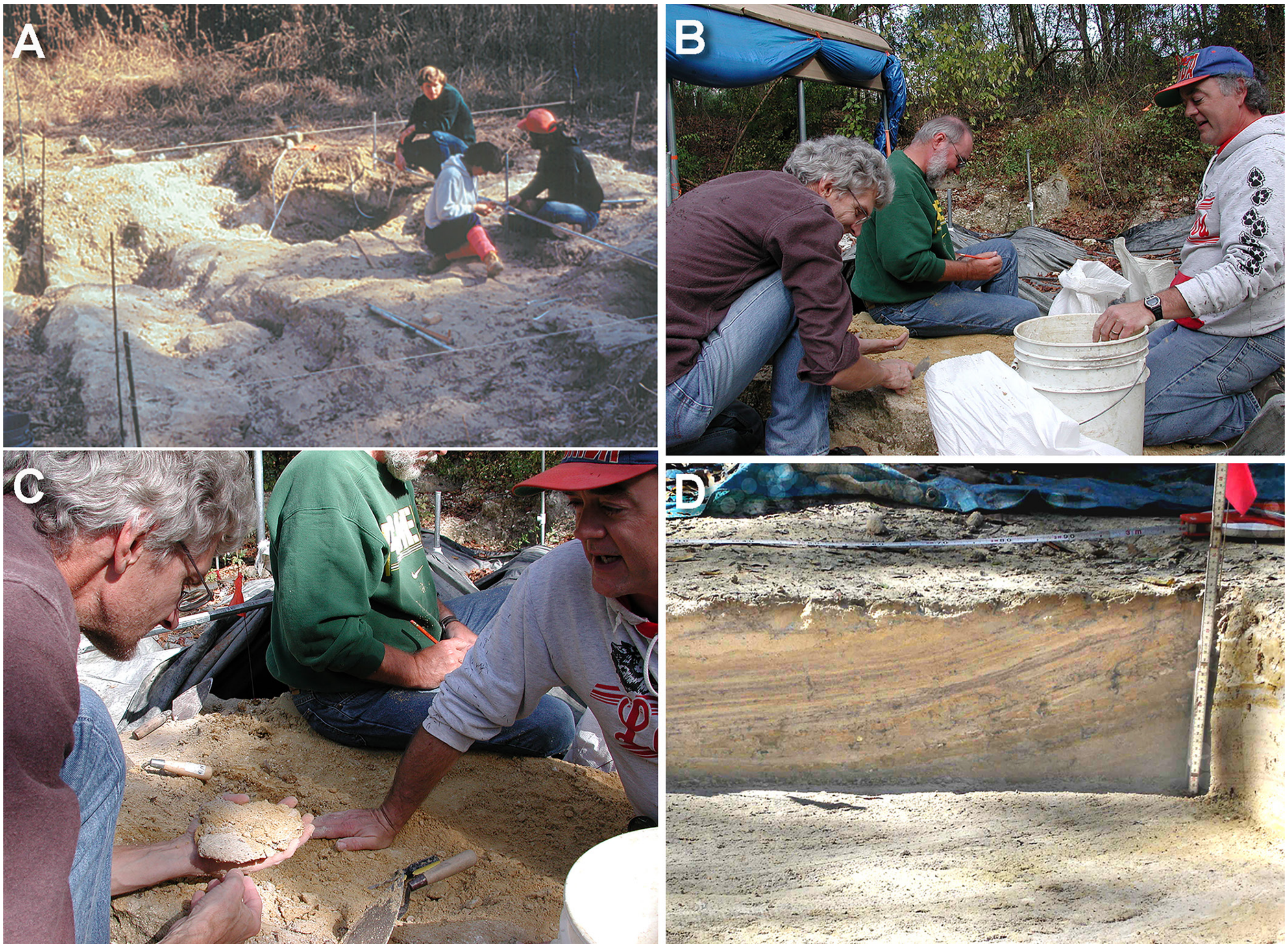

Figure 3. Field photographs of the early Miocene (early Hemingfordian) Thomas Farm Local Fauna, north of Bell, Gilchrist County, Florida. Thomas Farm is the type locality of the emballonurid bat *Floridopteryx poyeri*. A. View of a portion of the Thomas Farm site in the early 1980s showing the meter square grid system used to plot the location of larger fossils; from left to right, Steve Emslie, Ann Pratt, and Gary Morgan. B. Excavating sediment for screenwashing in 2001; from left to right, Nick Czaplewski, Art Poyer, and Gary Morgan. C. Close-up of a sample of the limesand layer, the richest sediment at Thomas Farm for bat fossils; from left to right, Nick Czaplewski (with sediment sample in hand), Art Poyer, and Gary Morgan. D. Wall of meter square showing thin layers of limesand sediment. Photos are courtesy of Richard Hulbert (A) and Erika Simons (B-D).

a diverse small vertebrate fauna of nearly 70 species, including frogs, toads, salamanders, lizards, snakes, birds, bats, shrews, and rodents. Small mammals include (Pratt, 1989; Pratt and Morgan, 1989): the soricid *Limnoecus* sp.; nine species of bats (see below); three sciurid rodents, *Petauristodon pattersoni* (type locality), *Nototamias hulberti* (type locality), and cf. *Miospermophilus* sp.; two heteromyid rodents, *Proheteromys floridanus* and *P. magnus*; and the eomyid rodent *Pseudotheridomys* sp. The biochronology of artiodactyls (Patton, 1969b), equids (Forstén, 1975; Hulbert and MacFadden, 1991), carnivorans (Tedford and Frailey, 1976; Wang et al., 1999), and sciurids (Pratt and Morgan, 1989) indicates a late early Hemingfordian age for Thomas Farm (late He1; ~17.5–18 Ma). The early Hemingfordian is defined in part by the first appearance of several genera of Eurasian immigrant carnivorans, including the amphicyonid *Amphicyon*, ursid *Hemicyon* (= *Phoberocyon*), and mustelid *Leptarctus*, as well as the first occurrence of the camelid *Floridatragulus* and the large flying squirrel *Petauristodon*, and the last occurrence of the amphicyonid *Cynelos* and the rhinocerotid *Menoceras* (Tedford and Frailey, 1976; Tedford et al., 1987, 2004; Pratt and Morgan, 1989). These genera are all present at Thomas Farm. *Amphicyon* and the equids *Anchitherium*, *Archaeohippus*, and *Parahippus* from Thomas Farm are very similar to species of these same genera from early Hemingfordian faunas in the Runningwater Formation of Nebraska. Other correlative early Hemingfordian faunas from the western United States are the Flint Hill LF of South Dakota and the Martin Canyon LF of Colorado (Tedford et al., 1987, 2004).

Thomas Farm has the largest bat sample from any Tertiary fossil deposit in North America, with more than 3,000 specimens (3,180 bat specimens as of 17 November 2022; UF/FLMNH vertebrate paleontology database). Most of the bat fossils consist of isolated teeth or ends of limb bones, but there are also numerous mandibles, maxillary fragments, and complete limb bones. The Thomas Farm chiropteran fauna is composed of at least nine species, including four species belonging to families with Neotropical affinities: one species of Emballonuridae, *Floridopteryx poyeri*, described here; one species of Natalidae, *Primonatalus prattae*, with Thomas Farm as the type locality (Morgan and Czaplewski, 2003); and two undescribed species of Molossidae similar to *Tadarida* (Czaplewski et al., 2003a). The other five species belong to the Vespertilionidae, three of which have been described, with Thomas Farm as the type locality, *Miomyotis floridanus* and *Suaptenos whitei* (Lawrence, 1943) and *Karstala silva* (Czaplewski and Morgan, 2000). Two other undescribed species of vespertilionids occur in the Thomas Farm LF based on differences in the morphology of the distal humerus with the three described vespertilionids from the site. One of these species is similar to tree bats of the genus *Lasiurus* and a second species is similar to big-eared bats of the genus *Corynorhinus*. Vespertilionids dominate the chiropteran fauna, with more than 75% of all bats belonging to *Suaptenos whitei*.

SYSTEMATIC PALEONTOLOGY

Order CHIROPTERA Blumenbach, 1779
Family EMBALLONURIDAE Gervais, 1855
***OLIGOPTERYX* new genus**

Type Species.—***Oligopteryx floridanus* sp. nov.**

Included Species.—Type species and *Oligopteryx hamaxitos*.

Diagnosis.—The m1 and m2 are nyctalodont, with the talonid significantly broader than the trigonid, paraconid and metaconid very close to one another, metaconid located anterior to the protoconid, postcristid at about a 45° angle to the long axis of tooth, entocristid blade-like and distinctly V-shaped with the apex of V oriented labially, and with a triangular-shaped process that projects posteroventrally from the posterior end of the mandibular symphysis below p4. M1 with a greatly reduced parastylar region, parastyle absent or very small, preparacrista very short, oriented posteriorly and running parallel to the postparacrista, paracingulum well developed, talon triangular in shape with a prominent posterolingual extension, metacingulum with a deep notch just posterior and lingual to the base of the metacone; in the M1 and M2 the talon basin is deeply concave, and in lingual view there is a deep V-shaped notch in the postprotocrista separating the protocone and the prominent, triangular hypocone.

Etymology.—*Oligo* (Greek), few, scanty, in reference to the Oligocene epoch, and *pteryx* (Greek), wing, a common ending for generic names in the family Emballonuridae.

OLIGOPTERYX FLORIDANUS **new species**

Fig. 4-10

Holotype.—UF 157769, right dentary fragment with p2, p4-m1, Brooksville 2 Local Fauna, late Oligocene (late early Arikareean), Hernando County, Florida.

Paratypes.—UF 157784, RM1; UF 182780, RM2; UF 182773, RM3 in maxillary fragment; UF 157790, left dentary fragment with m1-m2, p4 broken off at base of crown, and alveolus for p3; UF 157771, left dentary fragment with m2-m3; UF 179958, edentulous dentary with nearly complete horizonal ramus from anterior tip to m2 and all alveoli from c1-m2; UF 179904, left proximal humerus; UF 179964, left distal humerus; UF 179911, right proximal radius. All paratypes are from the Brooksville 2 Local Fauna, late Oligocene (late early Arikareean), Hernando County, Florida.

Referred Specimens.—Brooksville 2 Local Fauna.–Left M1 (7): UF 157776, 157779, 157785, 182777, 182779, 182858, 182896; right M1 (4): UF 157773, 157778, 182787, 182866; left M2 (2): UF 157780; 182781; right M2 (2): UF 157777, 182873; left M3 (6): UF 157775, 179991, 182774, 182775, 182778, 182899; right M3 (3): UF 157781, 182776, 182898; UF 157772, 157787, right dentary fragments with m3; UF 157789, right dentary fragment with m2; UF 182855, right dentary fragment with p4 and alveolus with root of p3; UF 182874, right dentary fragment with m2 and alveoli for p4 and m1; UF 157788, left dentary fragment with m2; left m1/m2 (9): UF 157782, 182814, 182861, 182862, 182864, 182868, 182871, 182891, 182893; right m1/m2 (13): UF 156289, 157783, 179987, 182809, 182811, 182813, 182819, 182859, 182860, 182865, 182867, 182870, 182892; UF 182872, left m3; right m3 (2): UF 182857, 182895; left C1: UF 182884; right c1: UF 182802; left P4: UF 182907, 182783; left proximal humerus (5): UF 179935, 179959, 179961, 179962, 179984; right proximal humerus (3): UF 179903, 179936, 179963; left distal humerus (5): UF 179909, 179965-179968; right distal humerus (2): UF 179910, 179939; left proximal radius (3): UF 179942, 179969, 179971; right proximal radius (6) UF 179912, 179913, 179940, 179972, 179981, 179982; left distal radius (2), UF 209956, 209957; right distal radius (4), UF 179926, 179944, 179974, 179975; left proximal femur, UF 182788. The minimum number of individuals (MNI) in the Brooksville 2 sample of *Oligopteryx floridanus* is seven based on the presence of seven left M1s and seven proximal ends of the right radius. The number of identifiable specimens (NISP) is 106.

I-75 Local Fauna.—UF 121701, 121702, right M1; UF 121704, left M2; UF 121703, right M2; UF 121724, partial right dentary with posterior half of p4 and alveoli for c1, p3, m1-m2; UF 16882, edentulous left dentary with alveoli for m1-m3; UF 121725, edentulous left dentary with alveoli for p3-m2; UF 121707, 121708, left m1/m2 (2); UF 121705, 121706, right m1/m2 (2); UF 121710, right distal humerus; UF 121711, 121712, left proximal radius (2). The MNI in the I-75 sample of *Oligopteryx floridanus* is two individuals based on the presence of two right M1s, two partial left dentaries, and two proximal ends of the left radius. The NISP is 14.

Type Locality and Age.—Brooksville 2 Local Fauna, late Oligocene (late early Arikareean; Ar3), Hernando County, Florida.

Occurrence.—Known only from the early Oligocene (Whitneyan) I-75 LF, Alachua County, Florida and the late Oligocene (early Arikareean) Brooksville 2 LF, Hernando County, Florida.

Etymology.—*floridanus*; in reference to the state of Florida, where all known specimens of this species have been collected.

Diagnosis.—Same as for the genus, with certain additional characters, mostly consisting of fea-

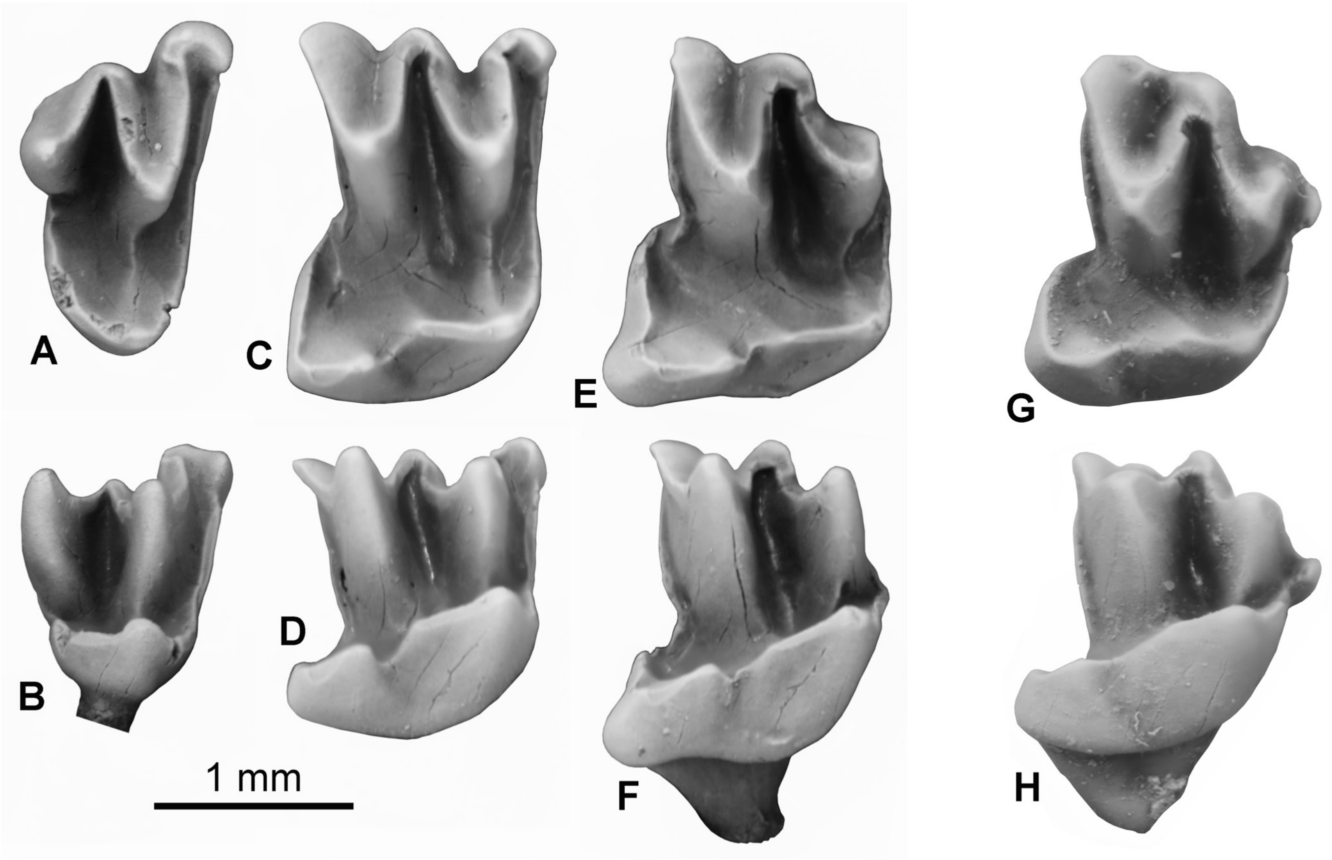

Figure 4. Right upper molars of *Oligopteryx floridanus* from Brooksville 2 LF (A-F) and *Karstopteryx gunnelli* from Buda LF (G-H). All molars in top row are occlusal views (A, C, E, G), all molars in bottom row are lingual views (B, D, F, H). A-B, *Oligopteryx floridanus*, UF 182773, M3 (paratype); C-D, *O. floridanus*, UF 182780, M2 (paratype); E-F, *O. floridanus*, UF 157784, M1 (paratype); G-H, *Karstopteryx gunnelli*, UF 97386, M1 (holotype).

tures that cannot be observed in the smaller species *Oligopteryx hamaxitos* because of the more limited sample of the latter (e.g., no lower premolars and M3/m3 of *O. hamaxitos* are known). The p2 is single-rooted, comparatively large, diamond-shaped, laterally compressed, and has a blade-like central cusp; the p3 is present, tiny, single-rooted, and located along the lingual margin of the mandibular toothrow; the p4 is tall, almost caniniform, with a conical central cusp, and triangular occlusal outline; the m3 with the talonid about the same breadth as the trigonid or slightly narrower, the cristid obliqua meets the trigonid near the labial base of the metaconid; the mandibular symphysis of the dentary is narrow anteriorly; M3 with a prominent hooked parastyle, metacone bulbous, posteriorly oriented, and more labially placed than the paracone, lacks a postmetacrista, metastyle, and hypocone, paraloph present.

Morphological Descriptions

Upper dentition.–Among both fossil and recent emballonurids, the M1 is one of the most diagnostic teeth. The sample of M1s of *Oligopteryx floridanus* from Brooksville 2 consists of 11 complete teeth (7 left, 4 right; measurements in Table 1). The following description is primarily based on UF 157784 (paratype; Fig. 4 E-F), a right M1 from Brooksville 2. However, the entire sample of M1s was used to evaluate dental variation. The overall shape of the M1 is shorter anteroposteriorly and more transversely elongated than in most other emballonurids. The M1 of the Florida fossils is somewhat rectangular with the long axis oriented

Table 1. Measurements of the upper molars of Oligocene and Miocene Emballonuridae from Florida, including: *Oligopteryx floridanus* and *O. hamaxitos* from the Oligocene I-75 LF (Whitneyan) and Brooksville 2 LF (early Arikareean), *Karstopteryx gunnelli* from the late Oligocene Buda LF (late Arikareean), and *Floridopteryx poyeri* from the early Miocene Thomas Farm LF (early Hemingfordian). All measurements are in mm. Missing measurement indicated by "—". Abbreviations for sample statistics: N (number of specimens); M (mean); OR (observed range). Statistics are calculated if there are three or more specimens for a particular tooth position.

Species, tooth position, fauna, and catalog number		anteroposterior length	transverse width
Oligopteryx floridanus			
M1			
Brooksville 2			
UF 157773		1.82	2.42
UF 157776		1.75	2.37
UF 157778		1.90	2.45
UF 157779		1.77	2.17
UF 157784 (paratype)		1.92	2.50
UF 157785		1.85	2.47
UF 182777		1.77	2.22
UF 182779		1.55	2.40
UF 182787		2.15	2.42
UF 182896		1.65	2.37
I-75			
UF 121701		1.65	2.42
	N	11	11
	M	1.80	2.38
	OR	1.55–2.15	2.17–2.50
M2			
Brooksville 2			
UF 157777		1.77	2.57
UF 157780		1.77	2.72
UF 182780 (paratype)		1.80	2.47
UF 182873		1.67	2.45
I-75			
UF 121703		1.70	2.42
UF 121704		1.72	2.62
	N	6	6
	M	1.74	2.54
	OR	1.67–1.80	2.42–2.72
M3			
Brooksville 2			
UF 157775		1.17	2.37
UF 157781		0.95	2.12
UF 179991		1.10	2.35
UF 182773 (paratype)		1.22	2.22
UF 182774		1.27	2.42
UF 182778		1.05	2.37
UF 182898		1.00	2.22
UF 182899		1.12	2.27
	N	8	8
	M	1.11	2.29
	OR	0.95–1.27	2.12–2.42

Table 1. (Cont.)

Species, tooth position, fauna, and catalog number	anteroposterior length	transverse width
Oligopteryx hamaxitos		
M1		
Brooksville 2		
UF 182808 (paratype)	1.37	1.65
M2		
Brooksville 2		
UF 157774	1.22	1.57
UF 157786 (paratype)	1.35	1.85
Karstopteryx gunnelli		
M1		
Buda		
UF 97386 (holotype)	1.75	2.27
Floridopteryx poyeri		
M1		
Thomas Farm		
UF 121134	0.85	–

labiolingually, while in most other emballonurids the M1 is squarish. The anterolabial region of the M1 labial to the paracone is highly reduced, almost lacking in some specimens. A parastyle is absent in most M1s from Brooksville but is present in several specimens consisting of a tiny cuspule at the anterolabial termination of the paracingulum (= precingulum). The only portion of the tooth present anterior to the mesostyle consists of the short preparacrista, paracone, and the postparacrista; the parastylar shelf labial to these structures is virtually absent. The parastylar region of the M1 is more reduced in *Oligopteryx* than in any living emballonurid. There is some variation in the length of the preparacrista in the sample of M1s from Brooksville, ranging from very short to moderate in length. In those teeth with a somewhat longer preparacrista (from a third to half the length of the postparacrista), this crest is oriented posteriorly, almost parallel to the postparacrista. In several M1s, the labialmost extension of the preparacrista is distinctly curved posteriorly. Posterior to the mesostyle, there is a shallow V-shaped notch in the metafossa labial to the metacone. The paracingulum is relatively broad, extending from the anterolabial base of the protocone to about the middle of the paracone, ending abruptly just anterior to the labial termination of the preparacrista. The protocone is located on the anterolingual margin and is oriented anteriorly, whereas the paracone and metacone are more vertical. About halfway between the protocone and the hypocone, there is a shallow but distinct triangular-shaped notch in the postprotocrista separating the two cusps. The hypocone is about half the height of the protocone and consists of a distinct low, rounded cusp. A weak paraloph extends from the tip of the protocone to the base of the paracone. A metaloph is absent. The trigon basin has a rather shallow, somewhat elliptical-shaped pit in its center that is deeper than the remainder of the basin but does not have sharply defined edges. The trigon basin is not nearly as deep or ‘pocketed’ as in some other emballonurids. The talon basin is deeper and better defined than the trigon basin, with the deepest portion posterior to the base of the metacone. The posterolabial portion of the talon basin is the posteriormost portion of the tooth, extending slightly farther posteriorly than the metastyle. The talon constitutes the posterolingual extension of the tooth, consisting of a well-developed, triangular-shaped process, ranging from sharply triangular to more broadly or bluntly triangular in some specimens. The narrow metacingulum (= postcingulum) extends from the base of the metacone to the metastyle. A deep, V-shaped notch separates the metacingulum from the more posteriorly and lingually placed talon basin.

A single right M1 of a large emballonurid from I-75 (UF 121701) is very similar to the Brooksville M1s. This tooth fits in the middle of the range of variation in most dental characters and size compared to the Brooksville sample (measurements in Table 1). A parastyle is absent, although there is a slight anterior bulge at the anterolabial termination of the paracingulum. The preparacrista is short, about one-third the length of and parallel to the postprotocrista. There is a very shallow indentation in the metafossa labial to the metacone. A weak paraloph is present and the metaloph is absent. There is a deep, V-shaped notch in the postprotocrista separating the protocone from the well-developed hypocone. The deeply concave talon basin extends posteriorly to the level of the metastyle. There is a V-shaped indentation in the metacingulum at the posterior base of the metacone.

There are seven M2s from Brooksville 2 (4 left, 3 right; measurements in Table 1). The following description is primarily based on UF 182780 (paratype; Fig. 4 C-D), a right M2. However, the entire sample of M2s was examined to evaluate dental variation. Unlike M1, the M2 of *Oligopteryx floridanus* has a well-developed parastyle that is hooked or curved. The preparacrista is also much better developed and longer than on M1, connecting the paracone to the parastyle. The paracingulum extends along the anterior margin of the tooth from the base of the protocone to the tip of the parastyle. There is a rather deep V-shaped notch in the labial margin of the parafossa labial to the paracone and a shallow notch in the metafossa labial to the metacone. The protocone and hypocone are separated by a rather deep, V-shaped notch in the postprotocrista. The hypocone is prominent and is positioned slightly more lingually than the protocone. A weak but distinct paraloph connects the protocone to the base of the paracone. A metaloph is absent in most specimens, but a weak metaloph connecting the posterior edge of the protocone to the base of the metacone is present in UF 157777. The trigon basin is relatively shallow for an emballonurid. The talon basin has a deep pit between the base of the metacone and the metacingulum. The talon is more squared off than in the M1 in which the talon is triangular. The metacingulum has a notch posterior to the base of the metacone, although this notch is not as deep as in the M1.

Two M2s of large emballonurids from I-75 (UF 121703, 121704) easily fit within the range of variation of M2s of *Oligopteryx floridanus* from Brooksville 2 (measurements in Table 1). The I-75 M2s have a strong, hooked parastyle. The paracingulum is broad and well developed. There is a fairly deep V-shaped notch in the parafossa labial to the paracone and a weak indentation in the metafossa labial to the metacone. There is a V-shaped notch between the protocone and hypocone. The hypocone is lingually offset. A weak paraloph is present, but no metaloph. The talon basin is deeply concave and the talon has a square posterior margin.

There are ten M3s from Brooksville 2 (6 left, 4 right; measurements in Table 1). The following description is primarily based on UF 182773 (paratype; Fig. 4 A-B), a right M3. The M3 of *Oligopteryx* is not as reduced as in some other emballonurids, in particular taphozoines that have a highly reduced M3. The only structures on the ectoloph of M3 that are lacking compared to the M2 are the postmetacrista and metastyle. There is a prominent hooked parastyle. A well-developed paracingulum extends from the base of the protocone to the parastyle. The paracone and metacone are about the same size and height, although the metacone is oriented slightly posteriorly. The paracone is sharply triangular in shape, whereas the metacone is more inflated or bulbous. The metacone is slightly more labially placed than the paracone, whereas the mesostyle is about a third of the distance between the parastyle and paracone, closer to the parastyle. By comparison, the mesostyle and parastyle are located at about the same level near the labial margin on M2. The premetacrista is noticeably shorter than the postparacrista because of the more labial position of the metacone. By comparison, the postparacrista and premetacrista are approximately the same length on M2. The metacone extends farther posteriorly than the posterior margin of the trigon basin. The talon and its basin are absent in M3, whereas the talon is the posteriormost portion of the tooth on M1 and M2. The protocone is low and rounded, located about midway along the lingual margin. A fairly strong paraloph extends from the protocone to the base of the paracone. A hypocone is absent, as is a metaloph. The trigon basin is rather shallow.

Isolated chiropteran canines are difficult to identify, and we have based our identification on a combination of size and similarity in morphology with other New World emballonurids. A C1 (UF 182884; Fig. 5 A-C) from the Brooksville 2 LF resembles the C1s of many other emballonurids in having anterior and posterior secondary cusps. It is larger than C1s referred to *Oligopteryx hamaxitos* described below. The secondary cusps are missing enamel and thus appear relatively weak, with the anterior one merged into the anterior crest of the main cusp, while the posterior one is separate yet connected with the posterior crest of the main cusp. In life, these secondary cusps would have been more prominent. The tooth lacks a labial cingulum and has a relatively weak lingual cingulum. The crown is rather hemiconical and labiolingually narrow, longer than wide, with a concave lingual face and a convex labial face. The root angles back from the crown base, giving a procumbent orientation to the tooth.

We refer two isolated P4s (UF 182783 and 182907; Fig. 6) from the Brooksville 2 local fauna to *Oligopteryx floridanus.* The P4s are three-rooted, with one root each supporting the central cusp (protocone), the posterolabial crest and style, and the lingual lobe. UF 182907 has a curved posterolabial crest, while UF 182783 has a slightly more sinuous posterolabial crest (but the latter might be due to greater wear in UF 182907). Both P4s have a relatively small lingual lobe (talon) with a shallow talon basin surrounded by a prominent cingulum. The anterior cingulum surrounding the base of the protocone is separated from the talon by an anterolingual notch, with anterolingual cingular cusps on either side of the notch. UF 182783 has a small swelling along the labial margin that is absent in UF 182907.

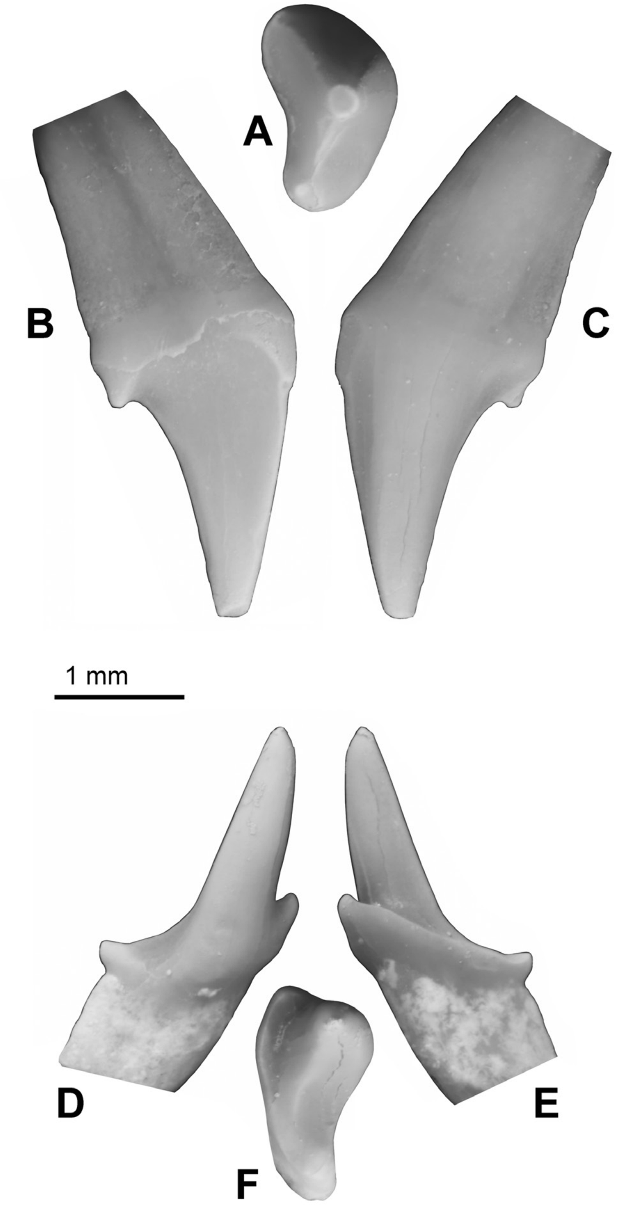

Figure 5. Canines referred to *Oligopteryx floridanus* from Brooksville 2 LF. A-C, UF 182884, left C1 in occlusal (A), lingual (B), and labial (C) views. D-F, UF 182802, right c1 in labial (D), lingual (E), and occlusal (F) views.

Lower Dentition.–None of the dentary fragments of *Oligopteryx floridanus* from Brooksville 2 or I-75 contains the canine, although these sites have a significant sample of isolated canines in the size range to belong to this species. An edentulous dentary from Brooksville 2 with alveoli for most of the lower teeth (UF 179958, paratype) is the only specimen in the sample that contains the alveolus for the lower canine. The c1 assigned to *Oligopteryx floridanus* (UF 182802; Fig. 5 D-F) from the Brooksville 2 LF has a tall, narrow main cusp that is aligned with the root but appears strongly canted forward relative to the basal cingulum and cingular cusps. The cingulum is absent labially but strong lingually, with prominent secondary cusps at the anterolingual and posterior ends. The base of the tooth is anteroposteriorly elongated and transversely narrowed, and the root is much more robust than the main cusp. The main cusp bears a longitudinal crest on its posterolingual face that does not connect with the lingual cingulum. The tooth is larger than the c1s of *O. hamaxitos* described below.

The presence of three lower premolars in *Oligopteryx* is the primitive condition in bats. The Eocene emballonurids *Tachypteron* and *Vespertiliavus* also have three lower premolars. However, extant emballonurids possess only two lower premolars; the intermediate premolar (p3) is absent. As discussed above under Methods and Materials, we identify the anteriormost lower premolar in bats that possess three lower premolars, including *Oligopteryx*, as the p2. We follow Miller (1907), Hand et al. (2015b), and Ciranello et al. (2016) in recognizing the three lower premolars in bats as p2, p3, p4, with p1 missing. There are two specimens of the p2 of *Oligopteryx floridanus*, one is preserved in the holotype dentary (UF 157769; Fig. 7 A-C) and the second is an isolated left p2. The p2 is relatively large and single-rooted, and laterally compressed with a large, blade-like central cusp, here regarded as the protoconid. It is sharply triangular in labial and lingual views and diamond-shaped in occlusal view. There is a weak lingual cingulum. The occlusal area is similar to that of p4, but in lateral view the protoconid of p2 is noticeably shorter. The posterior margin of p2 and anterior margin of p4 are in contact in the holotype, the only specimen that preserves both teeth.

Three dentaries of *Oligopteryx floridanus* from Brooksville 2 (UF 157790, 179958 [Fig. 8], 182855) and two from I-75 (UF 121723, 121724) preserve the tiny, round alveolus of a single-rooted p3, located along the lingual margin of the toothrow, wedged between the posterior edge of the alveolus for p2 and the anterior alveolus of p4. Several of these specimens have the root of p3, but none preserve the tooth crown. In one dentary (UF 182855), the p3 alveolus causes a slight indentation in the posterolingual margin of the p2 alveolus. No living emballonurid possesses a p3, although this tooth is present in the extinct Eocene genera *Tachypteron*

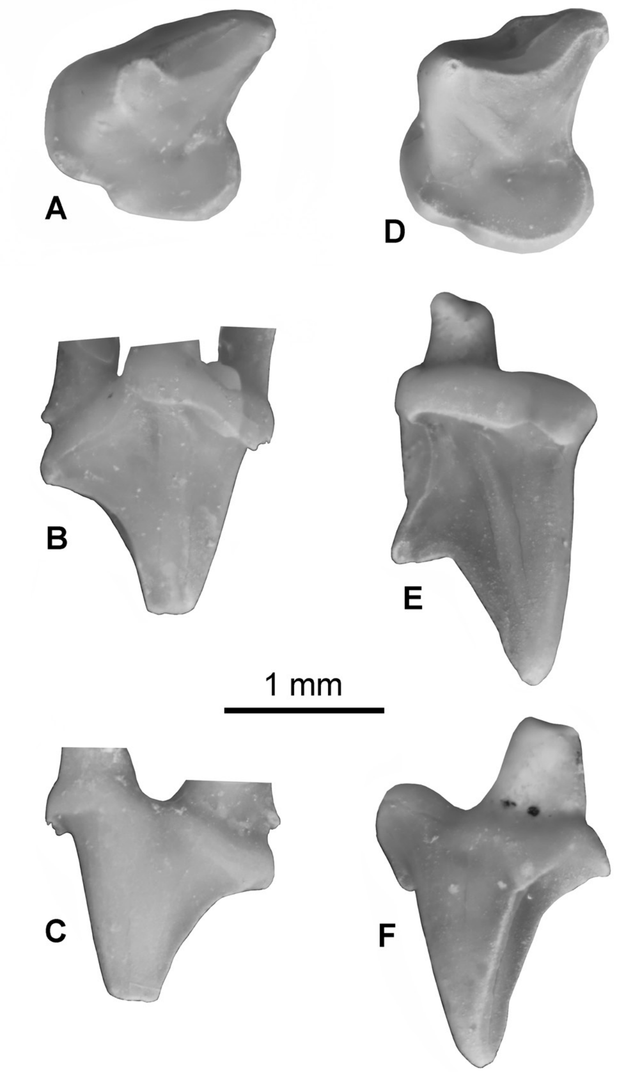

Figure 6. Left P4s referred to *Oligopteryx floridanus* from Brooksville 2 LF. A-C, UF 182907, left P4 in occlusal (A), lingual (B), and labial (C) views; D-F, UF 182783, left P4 in occlusal and slightly posterolingual (D), lingual and slightly anterior (E), and labial and slightly posterior (F) views.

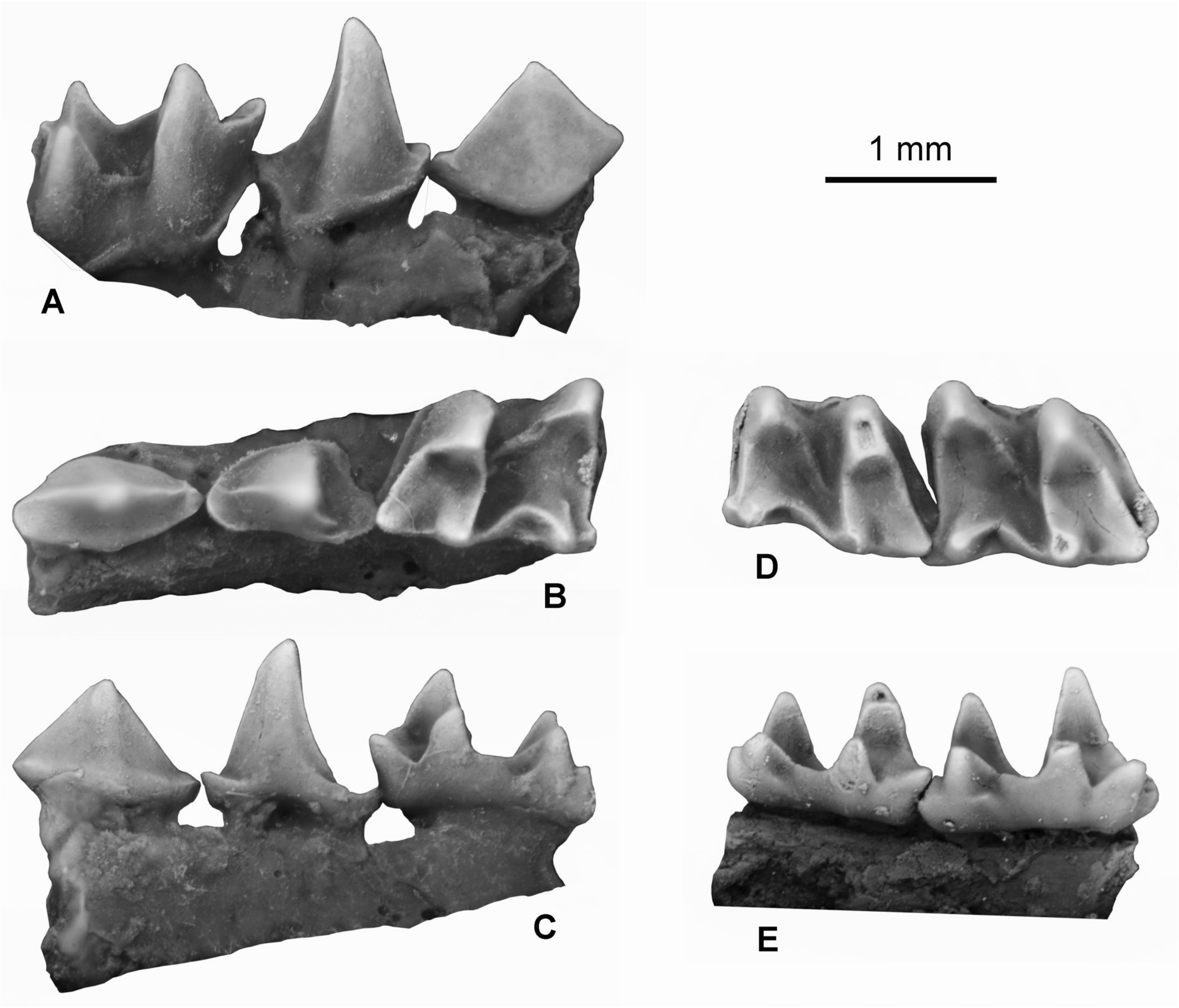

Figure 7. Lower teeth of *Oligopteryx floridanus* from Brooksville 2 LF. A-C, UF 157769 (holotype) right dentary fragment with p2, p4, and m1 in labial (A), occlusal (B), and lingual (C) views; D-E, UF 157771 left dentary fragment with m2-m3 in occlusal (D) and lingual (E) views.

and *Vespertiliavus*, as noted above.

Two partial dentaries from Brooksville 2 contain the p4 (UF 157769–holotype [Fig. 7A-C], 182855) and a partial p4 is present in a dentary fragment from I-75 (UF 121724). The p4 is double-rooted and has a very tall, conical central cusp that is somewhat caniniform in shape. The central cusp is noticeably taller than the m1 in the only specimen that preserves both teeth (UF 157769–holotype; Fig. 7 A-C). The occlusal outline is that of a rounded triangle, with the rounded apex of the triangle anterior and the posterior edge horizontal. The anterior edge of the conical central cusp slopes slightly anteriorly and has a distinct ridge extending from the apex almost to the anterior margin. The posterior edge of the central cusp is almost vertical. In occlusal view, there is a shallow but distinct basin between the central cusp and the posterior margin. There are well-developed labial, anterior, and posterior cingula. A small cuspid is present on the anterior cingulum, forming the anteriormost extension of p4. There is a distinct emargination or indentation along the anterolingual margin of p4 just posterior to the anterolingual cuspid. The posterior cingulum bears a cuspid at the posterolingual corner of the tooth.

The m1 and m2 of *Oligopteryx floridanus* are almost identical in size and morphology and cannot be reliably separated based on isolated teeth. Among the specimens from Brooksville 2, one dentary preserves both the m1 and m2 (UF 157790) and several other dentaries preserve either the m1 (UF 157769–holotype; Fig. 7 A-C) or the m2 (UF 157771; Fig. 7 D-E). There is also a significant sample of isolated m1s or m2s from Brooksville and several from I-75. Since the m1 and m2 are so similar, the following description pertains to both teeth. The m1/m2 are nyctalodont, the postcristid connects the hypoconid to the hypoconulid, with the latter cusp at the lingual margin of the tooth. The talonid is distinctly broader than the trigonid, and the talonid is also slightly longer than the trigonid anteroposteriorly. The paraconid and metaconid are located very close to one another along the lingual edge of the tooth, resulting from the anteroposterior compression of the trigonid. The metaconid is positioned noticeably anterior to the protoconid. The protocristid is oriented at an angle to the long axis of the toothrow, extending from the protoconid lingually and anteriorly to the metaconid. All four lingual cusps are rather low; the metaconid is the tallest, followed by the entoconid and paraconid, while the hypoconulid is the lowest. All except the hypoconulid are broadly conical, triangular-shaped, with rather blunt cusps. In lingual view, the metaconid and entoconid are oriented vertically, while the paraconid is oriented at about a 45° angle anteriorly. The labial cusps are taller than the lingual cusps, with the protoconid the tallest cusp on the m1 and m2, followed by the hypoconid. The cristid obliqua connects to the trigonid near the lingual base of the protoconid and lingual to the notch in the protocristid. In several specimens (e.g., UF 157771), the cristid obliqua meets the trigonid somewhat more labially, about midway between the protoconid and metaconid. The high, sharp entocristid in occlusal view has a V-shaped notch about halfway between the metaconid and entoconid, with the apex oriented labially. The small hypoconulid is located on the posterolingual corner of the tooth directly posterior to the larger entoconid. There is a basal labial cingulum extending from near the anterior margin around the protoconid along the base of the crown on the labial side of the tooth to the base of the hypoconid. The anterior labial cingulum is a well-developed but narrow shelf, terminating in an anterolabial cuspid located just anterior and labial to the paraconid. The cingulum labial to the protoconid and hypoconid is not as well developed as the anterior cingulum, especially compared to some other emballonurids. There is a weak postcingulum extending from the hypoconid to the base of the hypoconulid. A lingual cingulum is lacking.

Two dentaries from Brooksville 2 contain m3 (UF 157771 [Fig. 7 D-E], 157772) and there are also three isolated m3s from this site. Apart from its smaller size, the m3 is generally similar to the m1/m2, except for the following differences. The talonid on m3 is about the same breadth as the trigonid or is slightly narrower. The cristid obliqua forms a sharper angle with the long axis of the toothrow, meeting the trigonid farther lingually than on m1/m2, near the labial base of the metaconid. The entocristid is more broadly rounded labially, not as sharply V-shaped. The hypoconulid is smaller.

Oligopteryx floridanus is similar in size to the largest living New World emballonurid, *Diclidurus ingens*. It also compares well in size to the Old World *Taphozous melanopogon*, one of the larger extant emballonurids. The m1 and M1 lengths and humeral midshaft diameter of specimens (Tables 1, 2) provide estimates of its body weight of about 15.3 g to 24.1 g (by method of Gunnell et al., 2009).

Dentary.–The characters of the dentary of *Oligopteryx floridanus* are based primarily on an edentulous mandible from Brooksville 2 that preserves the alveoli for most of the lower teeth except the m3 (UF 179958–paratype; Fig. 8), as well as three edentulous dentary fragments from I-75. The ventral margin of the horizontal ramus is fairly straight below the molars and posterior to the sym-

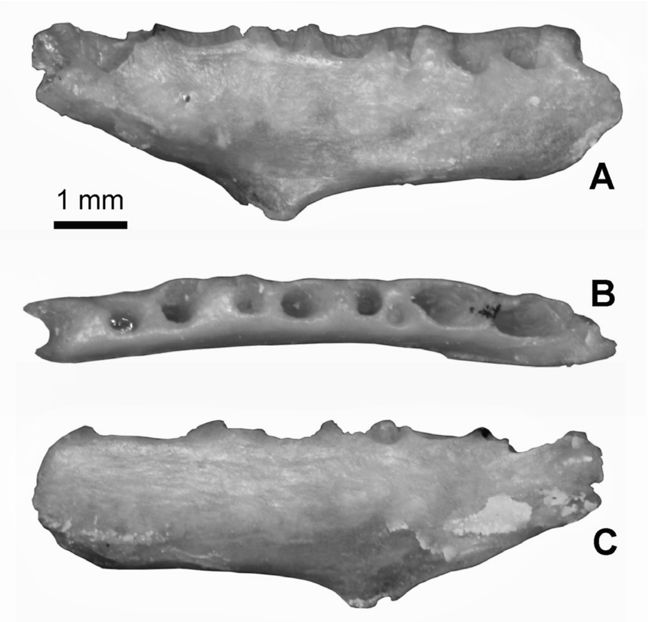

Figure 8. Edentulous partial horizontal ramus of dentary of *Oligopteryx floridanus* from Brooksville 2 LF. UF 179958, in labial (A), occlusal (B), and lingual (C) views.

physis. The anterior portion of the dentary below the incisors, canine, and p2 is shallow dorsoventrally. The mandibular symphysis extends posteriorly to about the level of p2. Along the ventral margin of the dentary there is a sharp, transversely narrow ridge or flange extending posteroventrally from the posterior edge of the symphysis to the level of p4. This ridge is triangular in lateral view with the apex of the triangle ventral to the anterior root of p4. The mental foramen is round and fairly small, located about halfway between the alveolar and ventral margins below the p2. The incisor alveoli are somewhat damaged, so it is not possible to determine the number of incisors present. The alveolus for the lower canine is large, about the same width as the alveolus for the p2 but somewhat longer. The canine alveolus is not round or elliptical as in most bats but is figure 8-shaped or kidney-shaped, consisting of a broader, more rounded anterior portion and a shorter, narrower posterior portion along the lingual margin of the toothrow. The anterior portion of the canine alveolus extends across the entire breadth of the toothrow, whereas the narrower posterior portion is lingually offset. The rounded alveolus for the single-rooted p2 is large, as broad as the canine alveolus but not as long. The tiny, round alveolus of the single-rooted p3 is located along the lingual margin, wedged between the posterior edge of the p2 alveolus and the anterior alveolus of the double-rooted p4.

A dentary fragment from I-75 (UF 16682) is the only specimen that preserves a portion of the ascending ramus posterior to the toothrow. The anterior edge of the coronoid process, the only portion of this process preserved, is located directly posterior to the m3, not lateral to the toothrow as in some other bats. Posterior to m3, the ascending ramus rises vertically such that the anterior edge of the coronoid process forms an angle of approximately 45° with the alveolar margin of the toothrow.

Petrosal.–A single left petrosal (UF 179902; Fig. 9A-D) is available from the Brooksville 2 Quarry and is tentatively referred to *Oligopteryx floridanus*. The petrosal is fairly intact except for the damage to the crista parotica, which is almost completely broken away exposing part of the lateral semicircular canal, and to the bone over the junction of the lateral and anterior semicircular canals. The fossil petrosal was compared with petrosals of modern Neotropical bats, in particular specimens of the emballonurids *Balantiopteryx plicata, Diclidurus albus, Peropteryx macrotis*, and *Saccopteryx bilineata* as representatives of the subfamily Emballonurinae, as well as a petrosal of a modern Afrotropical species, *Taphozous mauritianus* as a representative of the subfamily Taphozoinae, and of *Nycteris thebaica* as a representative of Nycteridae, the sister family to Emballonuridae (O'Leary et al., 2013; Teeling et al., 2018). Fig. 9 compares the petrosals of *O. floridanus* and *Peropteryx macrotis*.

The petrosal of *Oligopteryx* (UF 179902) is about the size of that in *Diclidurus albus* and *Taphozous mauritianus*, and larger than the petrosals of *Peropteryx macrotis, Saccopteryx bilineata*, and *Balantiopteryx plicata*. The specimen is referable to the family Emballonuridae by virtue of its close morphological resemblance to petrosals of extant emballonurids. In particular, the fossil petrosal shows a complete lamina between the three semi-

Table 2. Measurements of the lower premolars and molars of Oligocene and Miocene Emballonuridae from Florida, including: *Oligopteryx floridanus* and *O. hamaxitos* from the early Oligocene (Whitneyan) I-75 LF and the late Oligocene (early Arikareean) Brooksville 2 LF and *Floridopteryx poyeri* from the early Miocene (early Hemingfordian) Thomas Farm LF. For the lower premolars (p2 and p4), only two measurements were taken, anteroposterior length and maximum transverse width (recorded in the second column). For the lower molars (m1–m3), three measurements were taken, anteroposterior length, transverse width of the trigonid, and transverse width of the talonid. We were not able to positively identify the tooth position of isolated m1s or m2s, listed here as m1/m2. All measurements are in mm. Missing measurement indicated by "—". Abbreviations for sample statistics: N (number of specimens); M (mean); OR (observed range). Statistics are calculated if there are three or more specimens for a particular tooth position.

Species, fauna, tooth position, and catalog number		anteroposterior length	transverse width trigonid	transverse width talonid
Oligopteryx floridanus				
Brooksville 2				
p2				
UF 157769 (holotype)		1.45	0.75	–
p4				
UF 157769 (holotype)		1.30	0.85	–
UF 182855		1.47	0.97	–
m1				
UF 157769 (holotype)		1.77	1.20	1.32
UF 157790		1.67	1.15	1.25
m2				
UF 157771		1.80	1.30	1.40
UF 157788		1.72	1.22	1.30
UF 157789		1.67	1.27	1.45
UF 157790		1.62	1.20	1.27
UF 182874		1.75	1.22	1.30
	N	5	5	5
	M	1.71	1.24	1.34
	OR	1.62–1.80	1.20–1.30	1.27–1.45
m1/m2				
UF 156289		1.80	1.22	1.30
UF 157782		1.70	1.22	1.35
UF 157783		1.80	1.12	1.30
UF 179987		1.75	1.30	1.37
UF 182809		1.75	1.12	1.27
UF 182811		1.80	1.22	1.30
UF 182813		1.75	1.20	1.25
UF 182814		1.72	1.10	1.35
UF 182819		1.75	1.15	1.40
UF 182859		1.82	1.30	1.37
UF 182860		1.85	1.07	1.32
UF 182861		1.75	1.10	1.35
UF 182862		1.67	1.17	1.30
UF 182864		1.70	1.22	1.30
UF 182865		1.75	1.20	1.27
UF 182867		1.77	1.07	1.32
UF 182868		1.75	1.17	1.35
UF 182870		1.77	1.20	1.45
UF 182871		1.75	1.17	1.35
UF 182891		1.70	1.15	1.27
UF 182892		1.65	1.15	1.25
UF 182893		1.70	1.25	1.32
	N	22	22	22
	M	1.75	1.18	1.32
	OR	1.65–1.85	1.07–1.30	1.25–1.45

Table 2. Cont.

Species, fauna, tooth position, and catalog number		anteroposterior length	transverse width trigonid	transverse width talonid
Oligopteryx floridanus (cont.)				
I-75				
m1/m2				
UF 121705		1.70	1.10	1.10
UF 121706		1.77	1.30	1.42
UF 121707		1.72	1.05	1.10
UF 121708		1.72	1.20	1.35
	N	4	4	4
	M	1.73	1.16	1.24
	OR	1.70–1.77	1.05–1.30	1.10–1.42
Brooksville 2				
m3				
UF 157771		1.60	1.22	1.05
UF 157772		1.57	1.17	1.05
UF 157787		1.60	1.02	1.00
UF 182857		1.60	1.15	1.02
UF 182872		1.55	1.15	1.02
UF 182895		1.65	1.22	1.05
	N	6	6	6
	M	1.60	1.16	1.03
	OR	1.55–1.65	1.02–1.22	1.00–1.05
Oligopteryx hamaxitos				
Brooksville 2				
m1				
UF 157768 (holotype)		1.10	0.75	0.92
m2				
UF 157768 (holotype)		1.12	0.85	0.90
m1/m2				
UF 182817		1.25	0.80	0.90
UF 182869		1.27	0.82	0.92
Floridopteryx poyeri				
Thomas Farm				
m1				
UF 121132 (holotype)		1.52	0.92	1.12
m1/m2				
UF 121133		1.40	0.85	1.05
m3				
UF 108664		1.32	0.97	0.87

circular canals. This lamina is lacking in most families of bats in the Western Hemisphere except for Emballonuridae and some members of the Molossidae; it is shared with the Eastern Hemisphere Nycteridae. The fossil petrosal also has a complete lamina closing off the posterior semicircular canal with a few minuscule circular perforations (and a few tiny broken areas). The posterior semicircular canal is also completely laminated in *Peropteryx, Saccopteryx,* and *Balantiopteryx*. By contrast there is no lamina within the posterior semicircular canal in *Diclidurus* and *Taphozous*, and only a peripheral flange of lamina with a large central opening in *Nycteris*. The posterior semicircular canal is much smaller than either of the other two semicircular canals in the fossil and modern specimens.

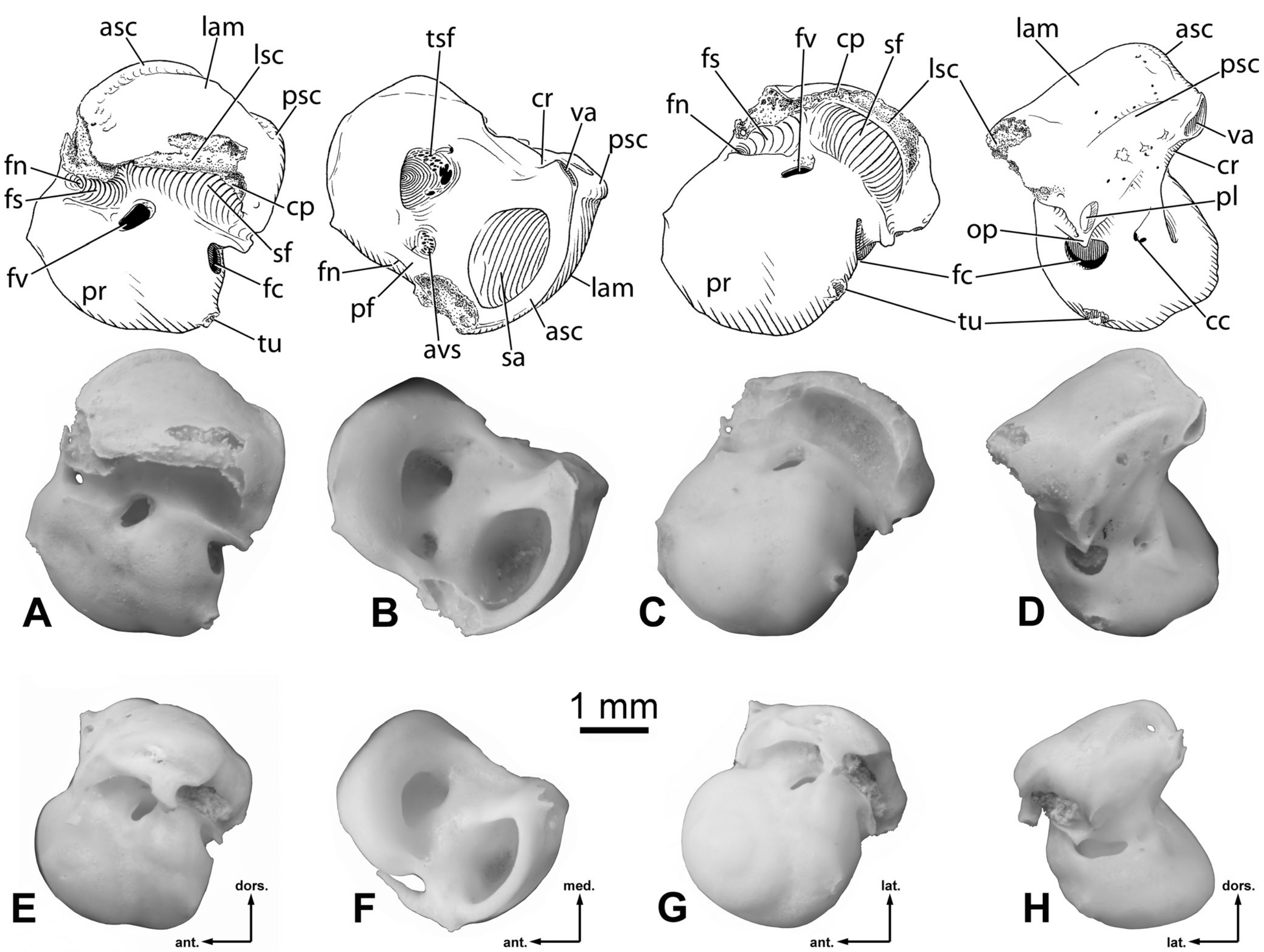

Figure 9. Petrosal bones of Emballonuridae. A-D, *Oligopteryx floridanus* from Brooksville 2, UF 179902, left petrosal with labeled interpretative drawings above and photographs below, in (A) lateral view, oriented with the lateral semicircular canal parallel to the horizon; (B) dorsal (endocranial) view; (C) ventrolateral view; and (D) posterior view. E-H, *Peropteryx macrotis*, modern specimen from Tikal, El Petén, Guatemala, UF Mammalogy 6935, left petrosal in views matching those of A-D. The fossa for the stapedius muscle is filled with organic matrix in the modern specimen. Orientation arrows indicate approximate anterior (ant.), dorsal (dors.), lateral (lat.), and medial (med.) directions. Abbreviations: ant, anterior; asc, anterior semicircular canal; avs, area vestibularis superior; cc, cochlear canaliculus (opening of cochlear aqueduct or perilymphatic duct); cp, crista parotica (damaged and mostly absent in the fossil); cr, common crus; dors, dorsal; fc, fenestra cochleae; fn, facial canal (for cranial nerve VII); fs, facial sulcus (semicanal for facial nerve); fv, fenestra vestibuli for footplate of stapes; lam, laminar cap between semicircular canals; lat, lateral; lsc, lateral semicircular canal; med, medial; op, process overhanging fenestra cochleae; pf, prefacial commissure; pl, platelike structure at lateral end of posterior semicircular canal; pr, promontorium of cochlea; psc, posterior semicircular canal; sa, subarcuate fossa; sf, fossa for stapedius muscle; tsf, spiral foraminous tract within the internal acoustic meatus; tu, small tubercle anteroventral to fenestra cochleae; va, opening of vestibular aqueduct; vent, ventral.

The fossil cochlea is phanerocochlear (having the petrosal wall thinly ossified such that the cochlear labyrinth is barely visible externally (Novacek 1985; 1991), as in all of the modern taxa examined. On the posteroventral surface of the cochlea is a small circular tubercle with a central hollow (Fig. 9, labeled “tu”); this tubercle is well developed also in *Balantiopteryx, Peropteryx, Diclidurus*, and *Taphozous* but is weaker in *Saccopteryx*. It is absent in *Nycteris*. The fenestra cochleae in UF 179902 in posterior view is wider than high, rounded ventrally and flat along its dorsal edge; it is larger than the fenestra vestibuli, as is also true in the other emballonurids examined except for *Diclidurus*, in which the two fenestrae are about the same size. The fenestra cochleae is more elongate in *Balantiopteryx*, *Saccopteryx*, and *Taphozous*, and especially elongate in *Peropteryx*. The fenestra cochleae is oval and higher than wide in *Nycteris*, about the same size as the fenestra vestibuli. Overhanging the fenestra cochleae in the fossil petrosal and the petrosals of all the recent emballonurids examined, there is a pointed process or flange of bone (Fig. 9 labeled "op"); this process occurs at the junction of the posterior and lateral semicircular canals. It includes a flangelike extension that runs anteriorly to form a partial floor beneath the stapedial fossa in all the emballonurids; this extension might enlarge the surface area for origin of the stapedius muscle. In the fossil, and in *Peropteryx*, *Saccopteryx* and *Balantiopteryx* the portion overhanging the fenestra cochleae occurs as a pointed or V-shaped process, whereas in *Diclidurus* it occurs as a long thin flange, and in *Taphozous* it is broader and rounded instead of pointed. Just dorsal and posterior to this process at the lateral base of the posterior semicircular canal, the fossil bears a relatively large, posteriorly facing, oval, flat platelike area that is slightly recessed (Fig. 9 labeled "pl"); this platelike area is about the same size and shape in *Taphozous* but twice the size in the fossil as in any of the other recent emballonurids. In *Peropteryx*, *Saccopteryx*, and *Balantiopteryx* it is situated similarly, but in *Diclidurus* it occurs behind a curved thin flange of bone. The petrosal of *Nycteris* completely lacks the process, flange, and platelike area seen in the emballonurids.

The prefacial commissure is relatively thick and transmits a moderate length of facial canal in UF 179902, *Taphozous*, and *Saccopteryx*, is thin and spans a short facial canal in *Balantiopteryx* and *Peropteryx*, and is thick and encloses a very long facial canal in *Diclidurus*. The area vestibularis superior occurs as a small, finely perforated, subcircular plate adjacent to the dorsal (endocranial) end of the facial canal in the fossil and all recent emballonurids. The facial canal is smaller in *Nycteris*, and the area vestibularis superior is even smaller.

The cochlear canaliculus is a small pore, much smaller than the fenestra vestibuli. The cochlear canaliculus is small in the recent emballonurids examined, too, and is situated closer to the fenestra cochleae in *Peropteryx* but about the same distance from the fenestra cochleae in the fossil as in *Balantiopteryx*, *Saccopteryx*, *Diclidurus*, and *Taphozous*.

In the fossil the external aperture of the vestibular aqueduct (Fig. 9 labeled "va") is large and rather slitlike, with an angled opening having its dorsal rim extending beyond the common crus while the posterior edge does not extend beyond the common crus. The structure is similar in *Peropteryx*, *Balantiopteryx*, *Saccopteryx,* and *Taphozous*. In *Diclidurus* both edges of the aperture extend equally beyond the common crus, and together extend somewhat farther than in the other emballonurids as a flattened tubelike structure, and the extension bears an adjacent flange of thin bone extending posteriad from the posterior side of the tubelike structure. In *Nycteris*, the aperture of the vestibular aqueduct is similarly slit-like but lacks a spout-like or funnel-like extension.

A number of important features occur on the crista parotica of bats (e.g., Morgan et al., 2019); unfortunately, these features cannot be examined or compared because of breakage of this structure in UF 179902.

Sulser et al. (2022) studied neuroanatomy of the cochlea in bats including two extant emballonurids (*Taphozous nudiventris* and *Coleura afra*). Their work examined the Rosenthal's canal wall for the spiral ganglion, which is perforated to varying degrees for the passage of fascicles of the cochlear nerve. The canal wall can be (1) perforated by many small holes for the nerve bundles (in which case it is called a "foraminal wall" or "tractus foraminosus" [and termed "spiral foraminous tract" in our Fig. 9B, labeled "tsf"]; this is the primitive condition of the entire tract in most mammals and non-echolocating bats), or (2) perforated by fewer larger holes (in which case it is called a "fenestral wall" or "tractus fenestralis"), or (3) widely open along its length (in which case it is called "wall-less"). These authors (Sulser et al., 2022) further defined the tracts along the spiral of the canal at the base (basal ½ turn, near the open portion of the internal acoustic meatus), middle (at the 1.5 cochlear turn), and apex (deep within the internal acoustic meatus near the apical turns). Among the two extant emballonurids examined, Sulser et al. (2022) found the tract in *C. afra* to be fenestrated in the base and middle, and wall-less nearer the apex. In *T. nudiventris*, they found a tractus foraminosus in the basal turn, tractus fenestralis in the middle, and wall-less condition in the apical portion. In the Oligocene fossil petrosal that we attribute to *Oligopteryx floridanus*, we note that the basal turn of the canal wall is foraminated (possibly partly damaged), whereas deeper turns are not visible with optical inspection and might require CT-scanning to properly characterize them.

The only other isolated petrosal available from an Oligocene bat in North America is that of the mormoopid *Koopmanycteris palaeomormoops* (UF 179901), described and illustrated by Morgan et al (2019), from the same site that produced the petrosal of *Oligopteryx floridanus,* the Brooksville 2 LF. Both *Oligopteryx* and *Koopmanycteris* have a phanerocochlear petrosal. The most obvious difference between the petrosal of *O. floridanus* and that of *Koopmanycteris* is the complete lamina between the semicircular canals that is absent in *K. palaeomormoops* (and other mormoopids). The petrosal of *O. floridanus* also has a lamina cap within the posterior semicircular canal (so that the only opening into the subarcuate fossa is through the anterior semicircular canal); in *Koopmanycteris* the posterior semicircular canal lacks a laminar cap or flanges. As noted above, *O. floridanus* has a Rosenthal's canal wall with a tractus foraminosus in its basal half turn; in *Koopmanycteris*, Rosenthal's canal wall is similarly foraminated in its basal and additionally in its middle turns, but the condition in the apical turns is not visible. *Koopmanycteris* lacks the small circular tubercle (Fig. 9, "tu") on the posteroventral surface of the cochlea; it also lacks the large pointed or V-shaped process that overhangs the fenestra cochleae in *Oligopteryx*. While the cochlear canaliculus in *O. floridanus* is much smaller than the fenestra vestibuli, the same opening in *Koopmanycteris* is about the same size as the fenestra vestibuli. While the external aperture of the vestibular aqueduct in *O. floridanus* (Fig.9, "va") is on a rather spoutlike tiny projection from the common crus, that in *Koopmanycteris* is not on a bony projection; instead, the aperture in *Koopmanycteris* is a small, curved slit along the common crus.

Humerus.–There are nine proximal ends and eight distal ends of the humerus of *Oligopteryx floridanus* from Brooksville 2 and a single distal humerus from I-75, although there are no complete specimens. The humeri are not directly associated with dental material. The association is based on the presence of large (and small) humeri that compare closely to humeri of modern members of the Emballonuridae, occurring together with teeth and dentaries that also represent large (and small) species belonging to the same family. The following description is based primarily on four well-preserved specimens, a proximal end of a left humerus (UF 179904, paratype), a proximal right humerus (UF 179936), a distal end of a left humerus (UF 179964, paratype; Fig. 10), and a distal right humerus (UF 179910) with more of the shaft preserved than UF 179964 but with some damage to the articular surface. The remainder of the sample was examined and used to help determine variation. All well-preserved proximal and distal ends of the humerus of *O. floridanus* were measured (Table 3).

In posterior view, the head on the proximal end of the humerus is elliptical in shape, somewhat transversely flattened, rounded distally, and more pointed or triangular proximally. The humeral head projects farther proximally than either the greater or lesser tuberosities. The head is not in the center of the shaft but is shifted noticeably laterally, located closer to the greater tuberosity than to the lesser tuberosity. The head is oriented at a slight angle to the shaft, canted distally toward the greater tuberosity. The greater tuberosity is rather elongated, rounded at its proximal end, and oriented at about a 45° angle to the shaft. The lesser tuberosity is considerably larger than the greater tuberosity, forming a large, triangular-shaped process with a squared-off proximal end. The greater and lesser

Table 3. Measurements of the humerus and radius of *Oligopteryx floridanus* and *O. hamaxitos* from the Oligocene Brooksville 2 LF (Arikareean) and I-75 LF (Whitneyan) of Florida. All measurements are in mm. Missing measurements are indicated by "–". Abbreviations for sample statistics: N (number of specimens); M (mean); OR (observed range). Statistics were calculated if there were three or more specimens for a particular limb element.

Element, species, site, and catalog number		proximal width	proximal depth	width of shaft	distal width maximum	distal width articular surface	distal depth
Humerus							
Oligopteryx floridanus							
Brooksville 2							
UF 179904 (paratype)		4.3	4.8	1.6	–	–	–
UF 179935		4.1	4.8	1.7	–	–	–
UF 179936		4.3	5.0	–	–	–	–
UF 179959		4.2	4.9	1.7	–	–	–
UF 179963		4.1	–	–	–	–	–
UF 179909		–	–	1.4	3.7	2.8	1.8
UF 179910		–	–	1.7	3.8	2.9	2.1
UF 179939		–	–	–	3.9	–	1.9
UF 179964 (paratype)		–	–	1.6	3.8	3.0	1.9
UF 179965		–	–	1.5	3.6	2.9	1.9
UF 179966		–	–	1.6	3.6	2.8	1.9
UF 179967		–	–	1.5	3.6	2.9	2.0
UF 179968		–	–	–	3.9	–	1.7
	N	5	4	9	8	6	8
	M	4.2	4.9	1.6	3.7	2.9	1.9
	OR	4.1–	4.8–	1.4–	3.6–	2.8–	1.7–
		4.3	5.0	1.7	3.9	3.0	2.1
I-75							
UF 121710		–	–	–	3.9	2.8	2.0
Oligopteryx hamaxitos							
Brooksville 2							
UF 182792 (paratype)		–	–	1.2	3.1	2.1	1.4
I-75							
UF 121714		–	–	1.3	2.8	2.3	1.5
Radius							
Oligopteryx floridanus							
Brooksville 2							
UF 179911 (paratype)		2.8	3.2	1.5	–	–	–
UF 179912		–	3.3	1.6	–	–	–
UF 179913		2.9	3.2	–	–	–	–
UF 179940		2.9	3.3	1.6	–	–	–
UF 179942		2.8	3.2	1.6	–	–	–
UF 179969		2.8	3.1	1.5	–	–	–
UF 179971		2.9	3.1	1.6	–	–	–
UF 179972		2.9	3.3	1.6	–	–	–
UF 179981		2.9	3.2	1.6	–	–	–
UF 179982		2.8	3.1	1.5	–	–	–
UF 179944		–	–	1.4	2.5	–	2.0
UF 179974		–	–	1.3	2.5	–	1.9
UF 179975		–	–	1.5	2.5	–	1.9
UF 209956		–	–	1.3	2.6	–	1.9
UF 209957		–	–	1.4	2.5	–	1.8
	N	9	10	14	5	–	5
	M	2.9	3.2	1.5	2.5	–	1.9
	OR	2.8–	3.1–	1.3–	2.5–	–	1.8–
		2.9	3.3	1.6	2.6	–	2.0
I-75							
UF 121711		3.0	3.2	–	–	–	–

Table 3. Cont.

Element, species, site, and catalog number		proximal width	proximal depth	width of shaft	distal width maximum	distal width articular surface	distal depth
Radius (cont.)							
Oligopteryx hamaxitos							
Brooksville 2							
UF 179914		2.0	2.1	1.2	–	–	–
UF 179915		2.1	2.2	1.1	–	–	–
UF 179983 (paratype)		2.1	2.2	1.1	–	–	–
UF 179977		–	–	1.1	2.1	–	1.4
	N	3	3	4	–	–	–
	M	2.1	2.2	1.1			
	OR	2.0– 2.1	2.1 2.2	1.1– 1.2			

tuberosities project about the same distance proximally. In proximal view, the pointed proximal portion of the head extends anteriorly to the base of the pectoral ridge. The larger size of the lesser tuberosity compared to the greater tuberosity is even more evident when viewed proximally. The lesser tuberosity is a prominent, triangular-shaped process extending medially, with a rounded anterior edge and straight posterior edge. It is about three times larger than the greater tuberosity. In this same view, the greater tuberosity is a narrow process with rounded edges, somewhat elongated in the anteroposterior dimension, with a shallow indentation about halfway along its length. The supraglenoid fossa is very shallow. In lateral view, the pectoral ridge is rather short but broad, triangular in shape, broader proximally. There is some variation in the shape of the pectoral ridge in the sample of proximal humeri from Brooksville 2; in most specimens this ridge is triangular but in several it is more rectangular. In medial view, the pectoral ridge bears a distinct, raised ridge that is oriented proximodistally, dividing the pectoral ridge into two approximately equal sections. There is a weak medial ridge on the shaft distal to the lesser tuberosity.

The distal articular surface of the humerus is slightly offset laterally from the shaft (Fig. 10). In anterior view, the lateral edge of the humeral shaft is in line with the weak groove separating the medial and lateral ridges of the capitulum, with the lateral ridge of the capitulum located lateral to the shaft. The lateral ridge of the capitulum is narrow transversely, occupying about one-fourth the breadth of the distal articular surface, but is deep in the proximo-distal dimension, extending proximally well beyond the medial ridge of the capitulum and trochlea. The medial ridge of the capitulum is large, bulbous, and somewhat spherical, composing about half the breadth of the distal articular surface. The medial and lateral ridges of the capitulum are separated by a shallow groove. The trochlea occupies about one-fourth the width of the distal articular surface and forms about a 45° angle with the medial ridge of the capitulum. The medial edge of the trochlea is essentially vertical and extends slightly farther distally than the capitulum. The medial ridge of the capitulum and trochlea are separated by a much deeper groove than the groove that separates the two parts of the capitulum. The medial epicondyle (epitrochlea), including the medial process of the epitrochlea and distal spinous process, is separated from the medial edge of the trochlea by a deep, rounded notch. Almost the entire medial epicondyle extends medial to the medial edge of the shaft. The medial process is well developed and rounded medially. The tip of the spinous process is sharply triangular and extends distally about half the distance between the proximal and distal edges of the articular surface, although this process is somewhat shorter in sever-

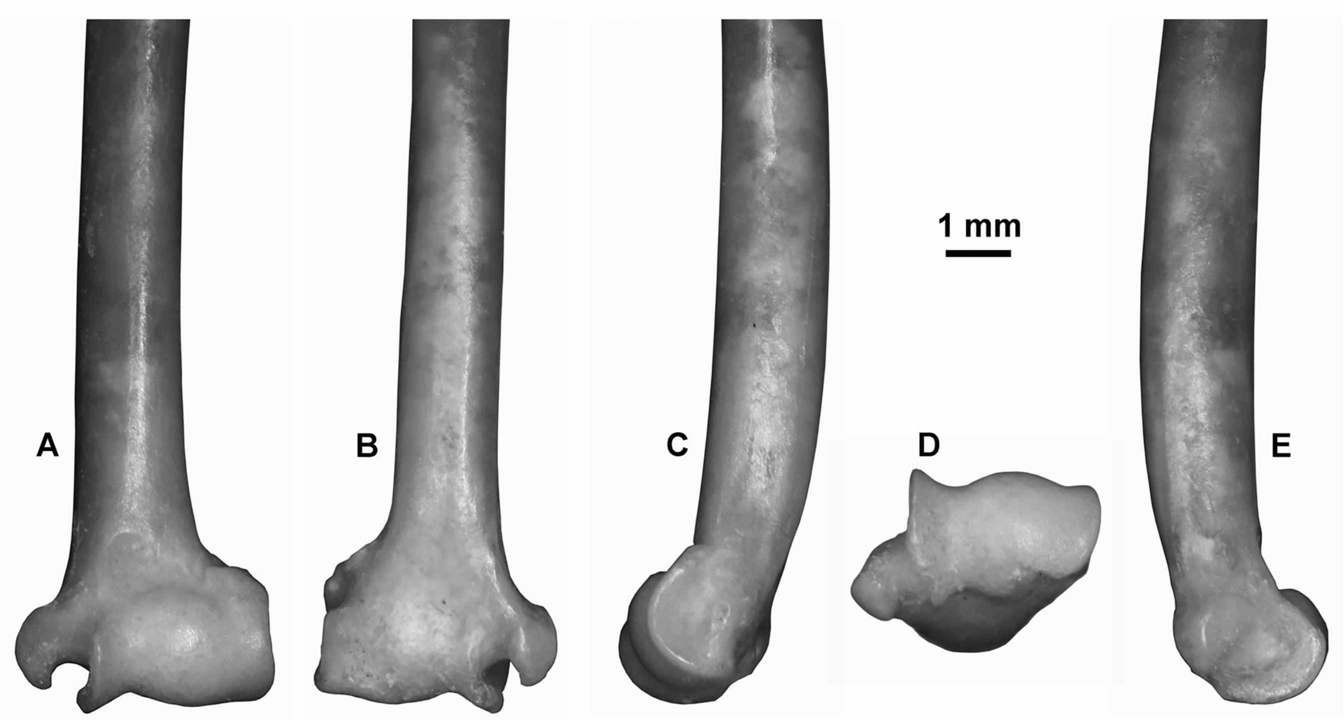

Figure 10. Distal portion of humerus of *Oligopteryx floridanus* from Brooksville 2 LF. UF 179964, in anterior (A), posterior (B), lateral (C), distal (D), and medial (E) views.

al specimens. The radial fossa is weak and shallow in most specimens, but in several humeri, including UF 179910, the radial fossa is deeper with distinct edges proximal to the trochlea. In posterior view, the small olecranon fossa varies from shallow to almost nonexistent. There are no ridges that extend distally from the medial and lateral margins of the shaft onto the distal articular surface and medial epicondyle. In medial view, the posterior edge of the spinous process is vertical or parallel to the shaft, whereas the anterior edge of this process angles posteriorly at about 45° toward the distal tip.

The humeri of *Oligopteryx floridanus* from Brooksville 2 and I-75, as well as several very similar humeri of the smaller *O. hamaxitos* from the same two sites, are identified as emballonurids by the elliptical and transversely flattened humeral head that angles distally toward the greater tuberosity, distal articular surface slightly offset laterally from the shaft, well-developed medial epicondyle bearing a strong distal spinous process separated from the trochlea by a deep rounded notch, and the large bulbous medial ridge of the capitulum. The distal articular surface of the humerus is more strongly offset laterally from the shaft in most other New World chiropteran families, including Mormoopidae, Phyllostomidae, Furipteridae, Thyropteridae, and Natalidae (Smith, 1972). In these families, the lateral ridge of the capitulum and at least a portion of the medial ridge of the capitulum are lateral to the humeral shaft, whereas in most emballonurids only the narrow lateral ridge is lateral to the shaft. In the Noctilionidae, the lateral ridge of the capitulum is more noticeably offset from the shaft and the central ridge of the capitulum is deeper but not as broad or as bulbous as in emballonurids. The distal articular surface is in line with the shaft in Vespertilionidae and Molossidae and the medial ridge of the capitulum is much narrower and almost ridge-like compared to the broader more bulbous medial ridge in emballonurids. Vespertilionids have a reduced distal spinous process compared to emballonurids. Some molossids have a well-developed distal spinous process but it is connected directly to the medial edge of the trochlea, not separated from the trochlea by a distinct notch as in emballonurids.

Radius.—There are 12 specimens of the proximal radius of *Oligopteryx floridanus*, ten from Brooksville 2 and two from I-75, as well as six distal radii from Brooksville. All of the complete proximal and distal ends of the radius were measured (Table 3). The proximalmost extension of the proximal radius has a gently rounded curvature, rather than consisting of a distinctly triangular-shaped process as in most other bats. The proximal articular surface consists of three slightly concave to nearly flat articular facets, corresponding to the three articular facets on the distal end of the humerus, the lateral and medial ridges of the capitulum and the trochlea. The facet for the medial ridge of the capitulum is a large, rounded concavity that occupies almost half of the proximal articular surface of the radius. The articular facet for the lateral ridge of the capitulum is shallower and narrower transversely but is taller or deeper in the proximodistal direction. The articular facet for the trochlea is nearly flat and consists of a narrow, medially directed process that is blunt or squared-off on its medial surface. Distal to the articular surface for the trochlea is a deep pit, the flexor fossa. There is a prominent ridge or flange along the medial edge of the shaft on the posterior surface distal to the flexor fossa. Two proximal radii from Brooksville 2 (UF 179911, paratype, 179912) preserve a considerably longer portion of the shaft than do the other specimens of the proximal radius. Both specimens consist of about the proximal one-third of the radius, preserving enough of the shaft to exhibit the very sharp bend or bowing of the shaft that is characteristic of emballonurids. In the complete radius of living emballonurids, this sharp bend occurs about one-third the distance between the proximal and distal ends. A sharp, narrow, raised ridge on the posterior surface of the shaft in UF 179912 marks the point where the thin, thread-like shaft of the ulna becomes fused with the radius, about halfway along the shaft but slightly closer to the proximal end. These two specimens also have a strong ridge along the medial edge of the shaft that extends from the flange distal to the flexor fossa distally beyond the break in the shaft. This ridge is strongest at midshaft.

The distal end of the radius is rather simple, exhibiting few morphological characters. We identified four distal radii of *Oligopteryx floridanus* from Brooksville 2, as well as a single distal radius of the smaller *O. hamaxitos* (described below). In anterior view, the distal edge of the articular surface is essentially straight, nearly horizontal to the shaft. There is a slight convexity representing the styloid process on the anterolateral edge of the articular surface. In posterior view, the distal edge of the articular surface forms a 45° angle to the shaft, trending distally from lateral to medial. The distal articular surface is deeply concave where it articulates with the lunar bone of the carpus. Just proximal to the lateral edge of the distal articular surface on the posterior surface of the shaft is a prominent, triangular-shaped, laterally oriented process that corresponds to the distalmost portion of the ulna.

The most obvious characters associating these radii with the Emballonuridae are the gently rounded proximalmost portion of the proximal articular surface and the strongly bent shaft about a third of the distance from the proximal end. In most other bats, the proximal extension of the radius is distinctly triangular in shape and the shaft is more gently curved. Except for their greater size, the fossil radii are very similar in morphology to the radius of living Neotropical emballonurids, such as *Peropteryx* and *Saccopteryx*. The only noticeable difference is the larger size and greater distal extension of the ridge or flange on the medial edge of the shaft just distal to the flexor fossa.

Femur.—A single proximal end of a femur of *Oligopteryx floridanus* was identified from the Brooksville 2 LF (UF 182788). This femur is easily distinguished from the proximal femur of the other common bat from Brooksville 2, the mormoopid *Koopmanycteris palaeomormoops*, by its larger size and much better development of the greater and lesser trochanters. The trochanters are highly reduced in mormoopids. Except for its larger size, the Brooksville emballonurid femur compares favorably with the femur of *Saccopteryx*. The femoral head of *Oligopteryx* is located in the center of the shaft, is generally spherical in shape although slightly flattened proximally, and bears a large centrally positioned fovea. The lesser trochanter is slightly larger than the greater trochanter and is somewhat triangular in shape, the greater trochanter is more pointed. The shaft is slightly bent laterally at the level of the medial ridge on the medial edge of shaft distal to the lesser trochanter.

Comparisons with other Emballonuridae

Considering the geographic proximity and general similarity in age, the most important comparisons of *Oligopteryx floridanus* from the early Oligocene (Whitneyan) I-75 LF and the late Oligocene (late early Arikareean) Brooksville 2 LF are with other Oligocene and early Miocene Emballonuridae from Florida, including *O. hamaxitos* from the same two localities as *O. floridanus*, *Karstopteryx gunnelli* from the latest Oligocene (early late Arikareean) Buda LF, and *Floridopteryx poyeri* from the early Miocene (early Hemingfordian) Thomas Farm LF. Next, we compare *O. floridanus* to the five extinct genera of Emballonuridae described from the Eocene, Oligocene, and Miocene of the Old World, *Afrillonura*, *Dhofarella*, *Pseudovespertiliavus*, *Tachypteron*, and *Vespertiliavus*. Table 4 lists comparative dental characters for the eight extinct genera of Emballonuridae, five from the Old World listed in the previous sentence (Ravel et al., 2016; Rosina and Pickford, 2021) and three from the New World (Florida) described here, *Oligopteryx*, *Karstopteryx*, and *Floridopteryx*. Although originally referred to the Emballonuridae by Hooker (1996), *Eppsinycteris* from the early Eocene of England is almost certainly not an emballonurid (Storch et al., 2002); it was placed in the Onychonycteridae by Smith et al. (2012). Finally, we compare *O. floridanus* to each of the 14 living genera of Emballonuridae (see list of modern comparative material examined in Appendix 1). Six extant species of emballonurids are also included in our analysis of dental characters in Table 4, including: two Old World species, *Taphozous melanopogon* (Taphozoinae) and *Coleura afra* (Emballonurinae: Emballonurini); and four New World species, *Balantiopteryx plicata*, *Diclidurus albus*, *Peropteryx macrotis*, and *Saccopteryx bilineata* (Emballonurinae: Diclidurini).

Comparisons with other extinct Emballonuridae from Florida.—Among the three other species of extinct Emballonuridae described here from the Oligocene and early Miocene of Florida, *Oligopteryx floridanus* is most similar to *O. hamaxitos*, both of which occur in the Oligocene Brooksville 2 and I-75 LFs, with the type specimens and largest samples of both species from Brooksville 2. *O. floridanus* differs from *O hamaxitos* primarily in its larger size (Tables 1–3). The mean anteroposterior length (1.80 mm) and transverse width (2.38 mm) of a sample of 11 M1s of *O. floridanus* are approximately 25-30% larger than those same two measurements in a paratype M1 of *O. hamaxitos* (1.37 mm, 1.65 mm, respectively). Except for the disparity in size, these two species are very similar in the morphology of the M1 and M2, with the main difference being the presence of a weak paraloph and absence of a metaloph in *O. floridanus* compared to a well developed paraloph and metaloph on both M1 and M2 in *O. hamaxitos*. There are also minor differences between these two species in the upper and lower canines and distal humerus that are discussed in more detail under the species account of *O. hamaxitos*.

Only the M1 of *Oligopteryx floridanus* can be compared to *Karstopteryx gunnelli* from the latest Oligocene Buda LF (Table 1), because the latter species is known from a single M1 (see below). *O. floridanus* and *K. gunnelli* are similar in size and in the reduction of the parastylar region of the M1, including the reduced parafossa labial to the paracone and the short preparacrista. However, *O. floridanus* can be readily distinguished from *K. gunnelli* in several other characters of the M1, including the absence of a parastyle, labial or posterior orientation of the preparacrista, rather strong V-shaped indentation in the labial margin of the metafossa, presence of a paraloph, location of the protocone on the anterolabial margin, prominent hypocone separated from the protocone by a distinct V-shaped notch in the postprotocrista, and an enlarged talon with a well developed, triangular-shaped, posterolingual extension. Other differences between the M1s of *O. floridanus* and *K.*

Table 4. Comparative dental characters in selected genera and species of Emballonuridae, including five extinct species from the Eocene, Oligocene, and Miocene of the Old World, three extinct species from the Oligocene and Miocene of the New World (Florida), and six extant species, two from the Old World and four from the New World. The five extinct Old World genera area listed first, in order from oldest/most primitive on the left (*Tachypteron*) to youngest on the right (*Afrillonura*), and next are the three extinct New World genera, also listed from oldest (*Oligopteryx*) to youngest (*Floridopteryx*). The extended portion of Table 4 includes six living genera, *Taphozous* and *Coleura* from the Old World and *Balantiopteryx*, *Diclidurus*, *Peropteryx*, and *Saccopteryx* from the New World. Characters 1-65 and character states in this table for *Tachypteron*, *Vespertiliavus*, *Pseudovespertiliavus*, and *Dhofarella* are from Ravel et al. (2016). Character states for *Afrillonura* are from Rosina and Pickford (2021) and character states for *Oligopteryx*, *Karstopteryx*, and *Floridopteryx* are from this study. For the new characters introduced in this study (Characters 66-85), we have scored the five extinct Old World genera based on the literature (e.g., Maitre, 2014; Ravel et al., 2016; Rosina and Pickford, 2021). Among our new characters, several cannot be evaluated in the extinct Old World genera because these characters are not illustrated or described in the literature. Characters for the six living species are based on examination of museum specimens in this study. See Appendix 2 for a more detailed explanation of the characters and character states listed in this table. The character states for each character are listed after the verbal description of each character in parentheses (e.g., 0, 1, 2). If a character is not preserved in a particular species because of incomplete fossil material, the character is listed as "?" (e.g., the M3 of *Floridopteryx poyeri* is not preserved, so characters of the M3, character numbers 62-65, are listed as "?"). If a character is absent from a particular species, the character is listed as "–" (e.g., *Floridopteryx poyeri* and all living species of Emballonuridae lack the p3, so characters of the p3, numbers 13 and 14, are listed as "–"). Abbreviations: E., Early, M., Middle, L., Late; N., north; S, south; SE, southeast; pen., peninsula; ant., anterior/anteriorly; post., posterior/posteriorly; lab., labial/labially; ling., lingual/lingually. Symbols: < less than; > greater than; = equal to.

Age, location, and characters	Extinct Genera of Emballonuridae							
	Old World					New World		
	Tachypteron franzeni[1]	*Vespertiliavus wingei*[2]	*Pseudo-vespertiliavus parva*	*Dhofarella* sigei/*D. thaleri* [3]	*Afrillonura namibensis*	*Oligopteryx floridanus*[4]	*Karstopteryx gunnelli*	*Floridopteryx poyeri*
Age	M. Eocene	M. Eocene- E. Oligocene	E.-M. Eocene	L. Eocene/ E. Oligocene	M. Miocene	E.-L. Oligocene	L. Oligocene	E. Miocene
Location	Europe Germany	Europe France	N. Africa Algeria	Egypt/ Oman	S. Africa Namibia	USA Florida	USA Florida	USA Florida
Characters from Ravel et al. (2016)								
Dentary								
1. Coronoid process height	high (0)	high (0)	?	?	?	?	?	low (1)
2. Coronoid process apex	sharp (0)	sharp (0)	?	?	?	?	?	sharp (0)
3. Horizontal ramus	gracile (0	robust (1)	?	?	?	robust (1)	?	robust (1)
4. Coronoid process angle	vertical (0)	oriented post. (1)	?	?	?	oriented post. (1)	?	oriented post. (1)
Lower dentition								
5. Lower incisor number	three (0)	three (0)	?	?	three (0)	?	?	?
6. Lower premolar number	three (0)	three (0)	?	?	?	three (0)	?	two (1)
7. Lower incisor lobes	bilobed (1)	?	?	?	?	?	?	?
8. Lower incisor relative size	equivalent (1)	?	?	?	?	?	?	?
9. c1 labial cingulum	strong (1)	strong (1)	?	?	strong (1)	absent (0)	?	?
10. c1 root/tubercle	straight (0)	straight (0)	?	?	straight (0)	straight (0)	?	?
11. c1 posterior basin	reduced (1)	extended post. (0)	?	?	extended post. (0)	extended post. (0)	?	?
12. p2 size	reduced (0)	not reduced (1)	?	?	not reduced (1)	not reduced (1)	?	?
13. p3 roots	two (1)	two (1)	?	?	?	one (0)	?	–
14. p3 crown	small (1)	small (1)	?	?	?	small (1)	?	–
15. p4 size	well developed (0)	well developed (0)	?	well developed (0)	well developed (0)	well developed (0)	?	?
16. p4 talonid	extended post. (0)	extended post. (0)	?	extended post. (0)	extended post. (0)	extended post. (0)	?	?
17. p4 paraconid	present (0)	absent (1)	?	absent (1)	absent (1)	absent (1)	?	?
18. p4 metaconid	absent (1)	absent (1)	?	absent (1)	absent (1)	absent (1)	?	?
19. lower molar trigonid cusps	high (0)	high (0)	high (0)	high (0)	high (0)	high (0)	?	high (0)
20. m1 trigonid	?	open lingually (0)	compressed (1)	open lingually (0)	compressed (1)	compressed (1)	?	compressed (1)
21. m2 trigonid	?	compressed (1)	compressed (1)	?	compressed (1)	compressed (1)	?	compressed (1)

Table 4. Cont.

Age, location, and characters	Extinct Genera of Emballonuridae							
	Old World					New World		
	Tachypteron franzeni[1]	*Vespertiliavus wingei*[2]	*Pseudo-vespertiliavus parva*	*Dhofarella* sigei/*D. thaleri* [3]	*Afrillonura namibensis*	*Oligopteryx floridanus*[4]	*Karstopteryx gunnelli*	*Floridopteryx poyeri*
Age	M. Eocene	M. Eocene-E. Oligocene	E.-M. Eocene	L. Eocene/ E. Oligocene	M. Miocene	E.-L. Oligocene	L. Oligocene	E. Miocene
Location	Europe Germany	Europe France	N. Africa Algeria	Egypt/ Oman	S. Africa Namibia	USA Florida	USA Florida	USA Florida
Lower dentition (cont.)								
22. m1 paraconid/metaconid distance	?	<metaconid/ entoconid (0)	>metaconid/ entoconid (1)	<metaconid/ entoconid (0)	<metaconid/ entoconid (0)	<metaconid/ entoconid (0)	? ?	<metaconid/ entoconid (0)
23. m2 paraconid/metaconid distance	?	<metaconid/ entoconid (0)	<metaconid/ entoconid (0)	?	<metaconid/ entoconid (0)	<metaconid/ entoconid (0)	? ?	<metaconid/ entoconid (0)
24. m3 paraconid/metaconid distance	?	<metaconid/ entoconid (0)	<metaconid/ entoconid (0)	?	<metaconid/ entoconid (0)	<metaconid/ entoconid (0)	? ?	<metaconid/ entoconid (0)
25. m1-m2 trigonid width	<talonid (0)	<talonid (0)	<talonid (0)	<talonid (0)	<talonid (0)	<talonid (0)	?	<talonid (0)
26. m1-m2 entoconid development	?	high (0)	moderate (2)	high (0)	high (0)	high (0)	?	high (0)
27. m1-m2 entocristid	?	straight (0)	straight (0)	curved (1)	curved (1)	curved (1)	?	curved (1)
28. m1-m2 cristid obliqua meets postcristid	?	medial (0)	lingual (1)	medial (0)	medial (0)	medial (0)	?	medial (0)
29. m1-m2 hypoconulid position	post. entoconid (2)	post. entoconid (2)	post. entoconid (2)	post. entoconid (2)	post. entoconid (2)	post. entoconid (2)	?	post. entoconid (2)
30. m1-m2 postcristid	straight (0)	straight (0)	straight/curved (0-1)	straight (0)	straight (0)	straight (0)	?	straight (0)
31. m3 talonid width	<trigonid (1)	<trigonid (1)	<trigonid (1)	?	<trigonid (1)	<trigonid (1)	?	<trigonid (1)
32. m3 hypoconulid	present (0)	weak/absent (1)	present (0)	?	weak/absent (1)	weak/absent (1)	?	weak/absent (1)
Upper dentition								
33. C1 labial cingulum	present (0)	?	present (0)	?	thin (2)	absent (1)	?	?
34. C1 lingual cingulum	curved (0)	?	straight (1)	?	curved (0)	straight (1)	?	?
35. C1 posterior cingulum break	present (0)	?	present (0)	?	absent (1)	absent (1)	?	?
36. number of upper premolars	three (1)	?	?	?	?	?	?	?
37. P4 talon basin	compressed (1)	compressed (1)	?	?	expanded ling. (0)	expanded ling. (0)	?	?
38. P4 crown, anterolabial lobe	pronounced (0)	absent (1)	?	?	weak ant-lab. lobe (2)	strong ant-lab. lobe (0)	?	`?
39. P4 anterolingual root/tubercle	present (0)	absent (1)	?	?	absent (1)	absent (1)	?	?
40. M1-M2 ectoflexus	double (0)	simple, ant. (1)	double/simple (0-1)	double (0)	simple, ant (1)	simple, ant (1)	simple, ant (1)	simple, ant (1)
41. M1-M2 V of ectoloph asymmetry	weak (1)	weak (1)	weak (1)	weak (1)	weak (1)	weak (1)	weak (1)	weak (1)
42. M1 inclination of labial margin	strong (0)	strong (0)	strong (0)	strong (0)	strong (0)	strong (0)	strong (0)	strong (0)
43. M1-M2 mesostyle position	lingual (1)	lingual (1)	lingual (1)	lingual (1)	lingual (1)	lingual (1)	lingual (1)	lingual (1)
44. M1-M2 labial cingulum	?	discontinuous (0)	discontinuous (0)	discontinuous (0)	discontinuous (0)	discontinuous (0)	discontinuous (0)	discontinuous (0)
45. M1-M2 labial cingulum at mesostyle	present (0)	present (0)	absent (1)	present (0)	absent (1)	absent (1)	absent (1)	absent (1)
46. M1 parastyle	connected (0)	connected (0)	connected/isolated (0-1)	isolated (1)	isolated (1)	absent (2)	isolated (1)	isolated (1)
47. M1-M2 paraloph	absent (1)	absent (1)	absent/present (0-1)	absent (1)	present (0)	present (0)	absent (1)	present (0)
48. M1-M2 metaloph	absent (1)	absent (1)	absent (1)	absent (1)	present (0)	absent (1)[5]	absent (1)	present (0)
49. M1-M1 paracingulum	wide (0)	wide (0)	wide (0)	wide (0)	wide (0)	wide (0)	wide (0)	wide (0)
50. M1-M2 metacingulum	thin (1)	thin (1)	thin (1)	wide (0)	thin (1)	thin (1)	thin (1)	?
51. M1-M2 protocone	well developed (0)	well developed (0)	well developed (0)	well developed (0)	reduced (1)	reduced (1)	reduced (1)	reduced (1)
52. M1-M2 postprotocrista connection	no connection (2)	lingual cingulum (1)	no connection (2)	lingual cingulum (1)	hypocone (3)	hypocone (3)	hypocone (3)	hypocone (3)
53. M1-M2 preprotocrista connection	precingulum (0)	precingulum (0)	precingulum (0)	precingulum (0)	precingulum (0)	precingulum (0)	precingulum (0)	precingulum (0)
54. M1-M2 protofossa extension	along ant.-post axis (0)	along ant.-post axis (0)	along ant.-post axis (0)	along ant.-post axis (0)	along ant.-post axis (0)	along ant.-post axis (0)	along ant.-post axis (0)	along ant.-post axis (0)
55. M1-M2 protofossa posterior opening	closed (0)	open (1)	open (1)	open (1)	open (1)	open (1)	open (1)	open (1)
56. M1-M2 level of protofossa	high (1)	high (1)	high (1)	low (0)	low (0)	low (0)	low (0)	low (0)
57. M1-M2 hypocone	absent (2)	absent (2)	small/absent (1-2)	absent (2)	well-developed (0)	well-developed (0)	small (1)	small (1)
58. M1-M2 posterior flattening of talon	weak (1)	weak (1)	strong/weak (0-1)	weak (1)	strong (0)	absent(2)/strong (0)[6]	absent (2)	strong (0)
59. M1-M2 posterior border of talon	rounded (0)	rounded (0)	rounded (0)	rounded (0)	post.ling. extension (1)	post.ling. extension (1)	rounded (1)	rounded (1)
60. M1-M2 orientation of talon	posterolingual (1)	posterior (0)	posterolingual (1)	posterior (0)	posterolingual (1)	posterolingual (1)	posterolingual (1)	posterolingual (1)
61. M1-M2 lingual cingulum	thick (0)	thick (0)	thick/thin (0-1)	thick (0)	thin (1)	absent (2)	absent (2)	absent (2)
62. M3 size	>½ width M2 (0)	>½ width M2 (0)	?	?	>½ width M2 (0)	>½ width M2 (0)	?	?

Table 4. Cont.

Age, location, and characters	Extinct Genera of Emballonuridae							
	Old World					New World		
	Tachypteron franzeni[1]	*Vespertiliavus wingei*[2]	*Pseudo-vespertiliavus parva*	*Dhofarella* sigei/*D. thaleri* [3]	*Afrillonura namibensis*	*Oligopteryx floridanus*[4]	*Karstopteryx gunnelli*	*Floridopteryx poyeri*
Age	M. Eocene	M. Eocene-E. Oligocene	E.-M. Eocene	L. Eocene/ E. Oligocene	M. Miocene	E.-L. Oligocene	L. Oligocene	E. Miocene
Location	Europe Germany	Europe France	N. Africa Algeria	Egypt/ Oman	S. Africa Namibia	USA Florida	USA Florida	USA Florida
Upper dentition (cont.)								
63. M3 metacone	small (0)	small (0)	?	?	well-developed (1)	well-developed (1)	?	?
64. M3 lingual cingulum	present (0)	absent (1)	?	?	absent (1)	absent (1)	?	?
65. M3 premetacrista	present (0)	present (0)	?	?	present (0)	present (0)	?	?
New characters (this study)								
Lower dentition								
66. c1 lingual cingulum	?	well developed (0)	?	?	well developed (0)	well developed (0)	?	?
67. c1 anterolingual cusp	?	present (0)	?	?	present (0)	present (0)	?	?
68. c1 posterolingual cusp	?	present (0)	?	?	present (0)	present (0)	?	?
69. p2 shape	rounded (0)	elongated (1)	?	?	rounded (0)	elongated (1)	?	?
70. p4 shape	rounded (0)	elongated (1)	?	elongated (1)	rounded (0)	elongated (1)	?	?
71. m1/m2 morphology	?	similar, open (0)	?	different (2)	similar, compressed (1)	similar, compressed (1)	?	similar, compressed
72. m1 trigonid	?	open lingually (0)	mod. compressed (1)	mod. compressed (1)	mod. compressed (1)	strongly compressed (2)	?	strongly compressed (2)
73. m1/m2 protoconid/metaconid placement	?	protoconid ant. to metaconid (0)	metaconid ant. to protoconid (1)	same level (2)	same level (2)	metaconid ant. to protoconid (1)	?	metaconid ant. to protoconid (1)
74. m1/m2 protocristid	?	post.-.ling. inclined from protoconid (1)	transverse (0)	transverse (0)	transverse (0)	ant.-ling.-inclined from protoconid (2)	?	ant.-ling.-inclined from protoconid (2)
75. m1/m2 entoconid	?	<metaconid	<metaconid	= metaconid (1)	?	= metaconid (1)	?	= metaconid (1)
76. m1/m2 hypoconulid	?	well developed (0)	well developed (0)	small (1)	well developed (0)	well developed (0)	?	well developed (0)
77. m1/m1 hypoconid/entoconid placement	?	same level (2)	same level (2)	same level (2)	entoconid ant. to hypoconid (1)	entoconid ant. to hypoconid (1)	? ?	entoconid ant. to hypoconid (1)
78. m1/m2 postcristid	?	transverse (0)	transverse (0)	transverse (0)	transverse (0)	ant.-ling.-inclined from hypoconid (2)	?	ant.-ling.-inclined from hypoconid (2)
79. m1/m2 labial cingulum	strong (0)	thin, continuous (1)	thin, continuous (1)	?	?	thin, continuous (1)	?	strong (2)
80. m3 talonid	?	narrow (1)	narrow (1)	narrow (1)	narrow (1)	broad (2)	?	broad (2)
81. m3 entoconid	?	small (1)	well developed (0)	well developed (0)	well developed (0)	well developed (0)	?	well developed (0)
Upper dentition								
82. C1 anterolingual cusp	?	absent (1)	absent (1)	?	present (0)	absent (1)/present (0)[7]	?	?
83. C1 posterolingual cusp	?	absent (1)	absent (1)	?	present (0)	present (0)	?	?
84. M1 parastylar region	unreduced (0)	unreduced (0)	unreduced (0)	reduced parastyle present (1)	reduced parastyle present (1)	reduced parastyle absent (2)	reduced parastyle present (1)	reduced parastyle present (1)
85. M1 preparacrista	weakly reduced (0)	weakly reduced (0)	weakly reduced (0)	short (1)	very short/absent (2)	short (1)	short (1)	short (1)

[1] Very few of our "new characters" (characters 66–85) can be evaluated for *Tachypteron franzeni* because the upper and lower jaws of the type and paratype are firmly occluded with only a lateral/labial view visible (Storch et al., 2002). Occlusal and lingual characters of the teeth cannot be evaluated.

[2] There are at least ten described species of *Vespertiliavus* from the late Eocene and early Oligocene of Europe (France) and the early to middle Eocene of Tunisia in North Africa (Ravel et al., 2016). We chose *V. wingei* to be representative of *Vespertiliavus* because it is more completely known than the other species in the genus. Character states 66-85 are from Maitre (2014).

[3] The genus *Dhofarella* is incompletely known, so we include characters from both described species in this genus, *D. sigei* from the late Eocene of Egypt (Gunnell et al. (2008) and *D. thaleri* from the early Oligocene of Oman (Sigé et al., 1994).

[4] With a few minor exceptions (see text), all characters listed here for *Oligopteryx floridanus* also apply to the second, smaller species in this genus, *O. hamaxitos*, described in this paper.

[5] A metaloph is present on both the M1 and M2 of the smaller species *Oligopteryx hamaxitos*, one of the few dental differences with *O. floridanus*.

[6] The M1 and M2 of *Oligopteryx floridanus* differ strongly in this character; the M1 has a posterior extension of the talon and shows no posterior flattening, whereas the M2 has a flattened posterior border of the talon.

[7] An anterolingual cusp is absent on the C1 of *Oligopteryx floridanus* but present on *O. hamaxitos*.

Table 4. (Extended).

Age, location, and characters	Extant Species of Emballonuridae					
	Old World		New World			
	Taphozous melanopogon	*Coleura afra*	*Balantiopteryx plicata*	*Diclidurus albus*	*Peropteryx macrotis*	*Saccopteryx bilineata*
Age	Living	Living	Living	Living	Living	Living
Geographic distribution	India, SE Asia Philippines	Africa	N. Mexico to Costa Rica	S. Mexico to South America	S. Mexico to South America	S. Mexico to South America
Characters from Ravel et al. (2016)						
Mandibular characters						
1. Coronoid process height	high (0)	high (0)	high (0)	high (0)	high (0)	high (0)
2. Coronoid process apex	sharp (0)	sharp (0)	sharp (0)	sharp (0)	sharp (0)	sharp (0)
3. Horizontal ramus	robust (1)	robust (1)	robust (1)	robust (1)	robust (1)	gracile (0)
4. Coronoid process angle	vertical (0)	vertical (0)	vertical (0)	vertical (0)	vertical (0)	vertical (0)
Lower dentition						
5. Lower incisor number	two (1)	three (0)	three (0)	three (0)	three (0)	three (0)
6. Lower premolar number	two (1)	two (1)	two (1)	two (1)	two (1)	two (1)
7. Lower incisor lobes	trilobed (1)	trilobed (1)	trilobed (1)	trilobed (1)	trilobed (1)	trilobed (1)
8. Lower incisor size	all equivalent (0)	all equivalent (0)	all equivalent (0)	all equivalent (0)	all equivalent (0)	all equivalent (0)
9. c1 labial cingulum	well developed (0)	well developed (0)	well developed (0)	well developed (0)	thin/absent (1)	thin/absent (1)
10. c1 root	straight (0)	straight (0)	straight (0)	straight (0)	straight (0)	straight (0)
11. c1 posterior basin	extended post. (0)	extended post. (0)	reduced (1)	reduced (1)	reduced (1)	reduced (1)
12. p2 size	>p4 (2)	reduced (0)	reduced (0)	reduced (0)	reduced (0)	reduced (0)
13. p3 roots	–	–	–	–	–	–
14. p3 crown	–	–	–	–	–	–
15. p4 size	well developed (0)	well developed (0)	well developed (0)	well developed (0)	well developed (0)	well developed (0)
16. p4 talonid	extended post. (0)	reduced (1)	reduced (1)	extended post. (0)	reduced (1)	extended post. (0)
17. p4 paraconid	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)
18. p4 metaconid	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)
19. lower molar trigonid cusps	high (0)	high (0)	high (0)	high (0)	high (0)	high (0)
20. m1 trigonid	ling. open (0)	compressed (1)	compressed (1)	ling. open (0)	compressed (1)	compressed (1)
21. m2 trigonid	ling. open (0)	compressed (1)	compressed (1)	compressed (1)	compressed (1)	compressed (1)
22. m1 paraconid/metaconid	>metaconid/entoconid (1)	<metaconid/entoconid (0)	<metaconid/entoconid (0)	>metaconid/entoconid (1)	<metaconid/entoconid (0)	<metaconid/entoconid (0)
23. m2 paraconid/metaconid	<metaconid/entoconid (0)	<metaconid/entoconid (0)	<metaconid/entoconid (0)	<metaconid/entoconid (0)	<metaconid/entoconid (0)	<metaconid/entoconid (0)
24. m3 paraconid/metaconid	<metaconid/entoconid (0)	<metaconid/entoconid (0)	<metaconid/entoconid (0)	<metaconid/entoconid (0)	<metaconid/entoconid (0)	<metaconid/entoconid (0)
25. m1-m2 trigonid width	<talonid (0)	<talonid (0)	<talonid (0)	<talonid (0)	<talonid (0)	<talonid (0)
26. m1-m2 entoconid	moderate (2)	high (0)	moderate (2)	high (0)	moderate (2)	high (0)
27. m1-m2 entocristid	straight (0)	strongly curved (2)	strongly curved (2)	slightly curved (1)	strongly curved (2)	strongly curved (2)
28. m1-m2 cristid obliqua meets trigonid	lingual (1)	(0) midpoint	(0) midpoint	(2) labial	(2) labial	(2) labial
29. m1-m2 hypoconulid	post. entoconid (2)	post. entoconid (2)	post. entoconid (2)	post. entoconid (2)	post. entoconid (2)	post. entoconid (2)
30. m1-m2 postcristid	straight (0)	straight (0)	straight (0)	straight (0)	straight (0)	straight (0)
31. m3 talonid width	<trigonid (1)	<trigonid (1)	<trigonid (1)	<trigonid (1)	<trigonid (1)	<trigonid (1)
32. m3 hypoconulid	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)
Upper dentition						
33. C1 labial cingulum	present (0)	present (0)	absent (1)	present (0)	absent (1)	absent (1)
34. C1 lingual cingulum	straight (1)	straight (1)	curved (0)	straight (1)	straight (1)	straight (1)
35. C1 posterior cingulum break	present (0)	present (0)	present (0)	absent (1)	present (0)	present (0)
36. Number of upper premolars	two (1)	two (1)	two (1)	two (1)	two (1)	two (1)
37. P4 talon basin	compressed (1)	expanded (0)	expanded (0)	expanded (0)	expanded (0)	compressed (1)
38. P4 crown, anterolabial lobe	pronounced (0)	pronounced (0)	lacks ant.-lab. lobe (1)	lacks ant.-lab. lobe (1)	lacks ant.-lab. lobe (1)	lacks ant.-lab. lobe (1)
39. P4 anterolingual root/tubercle	absent (1)	absent (1)	present (0)	present (0)	present (0)	present (0)
40. M1-M2 ectoflexus	double (0)	double (0)	double (0)	double (0)	double (0)	double (0)
41. M1-M2 V of ectoloph	pronounced (1)	pronounced (1)	pronounced (1)	pronounced (1)	pronounced (1)	pronounced (1)

Table 4. (Extended).

Age, location, and characters	Extant Species of Emballonuridae					
	Old World		New World			
	Taphozous melanopogon	*Coleura afra*	*Balantiopteryx plicata*	*Diclidurus albus*	*Peropteryx macrotis*	*Saccopteryx bilineata*
Age	Living	Living	Living	Living	Living	Living
Geographic distribution	India, SE Asia Philippines	Africa	N. Mexico to Costa Rica	S. Mexico to South America	S. Mexico to South America	S. Mexico to South America
Upper dentition (cont.)						
42. M1 inclination of labial margin	strong (0)	strong (0)	strong (0)	strong (0)	strong (0)	strong (0)
43. M1-M2 mesostyle position	labial (1)	labial (1)	labial (1)	labial (1)	labial (1)	labial (1)
44. M1-M2 labial cingulum	discontinuous (0)	discontinuous (0)	discontinuous (0)	discontinuous (0)	discontinuous (0)	discontinuous (0)
45. M1-M2 labial cingulum at mesostyle	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)
46. M1 parastyle	connected (0)	isolated (1)	absent (2)	isolated (1)	isolated (1)	isolated (1)
47. M1-M2 paraloph	absent (1)	absent (1)	present (0)	present (0)	present (0)	present (0)
48. M1-M2 metaloph	absent (1)	absent (1)	present (0)	absent (1)	absent (1)	present (0)
49. M1-M1 paracingulum	thin/absent (1)	wide (0)	wide (0)	wide (0)	wide (0)	wide (0)
50. M1-M2 metacingulum	thin (1)	wide (0)	wide (0)	wide (0)	wide (0)	wide (0)
51. M1-M2 protocone	well developed (0)	well developed (0)	well developed (0)	well developed (0)	well developed (0)	well developed (0)
52. M1-M2 postprotocrista connection	ling. cingulum (1)	hypocone (3)	hypocone (3)	hypocone (3)	hypocone (3)	hypocone (3)
53. M1-M2 preprotocrista connection	paracone (1)	paracingulum (0)	paracingulum (0)	paracingulum (0)	paracingulum (0)	paracingulum (0)
54. M1-M2 protofossa extension	along ant.-post. axis (0)	along ant.-post. axis (0)	along ant.-post. axis (0)	along ant.-post. axis (0)	along ant.-post. axis (0)	along ant.-post. axis (0)
55. M1-M2 protofossa posterior opening	open (1)	open (1)	open (1)	open (1)	open (1)	open (1)
56. M1-M2 level of protofossa	low (0)	low (0)	low (0)	low (0)	low (0)	low (0)
57. M1-M2 hypocone	absent (2)	low/weak (1)	well developed (0)	well developed (0)	well developed (0)	low/weak (1)
58. M1-M2 posterior flattening of talon	weak (1)	strong (0)	strong (0)	strong (0)	strong (0)	strong (0)
59. M1-M2 posterior border of talon	rounded (0)	w/post.-ling. lobe (1)	w/post.-ling. lobe (1)	w/post.-ling. lobe (1)	w/post.-ling. lobe (1)	w/post.-ling. lobe (1)
60. M1-M2 orientation of talon	posterior (0)	post.-ling. (1)	post.-ling. (1)	post.-ling. (1)	post.-ling. (1)	post.-ling. (1)
61. M1-M2 lingual cingulum	thick (0)	thin/absent (1)	thin/absent (1)	thin/absent (1)	thin/absent (1)	thin/absent (1)
62. M3 size	<½ width M2 (1)	>½ width M2 (0)	>½ width M2 (0)	>½ width M2 (0)	>½ width M2 (0)	>½ width M2 (0)
63. M3 metacone	absent (2)	well developed (1)	well developed (1)	well developed (1)	well developed (1)	well developed (1)
64. M3 lingual cingulum	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)	absent (1)
65. M3 premetacrista	absent (1)	present (0)	present (0)	present (0)	present (0)	present (0)
New characters (this study)						
Lower dentition						
66. c1 lingual cingulum	well developed (0)	well developed (0)	well developed (0)	well developed (0)	well developed (0)	well developed (0)
67. c1 anterolingual cusp	absent (1)	present (0)	present (0)	absent (1)	absent (1)	present (0)
68. c1 posterolingual cusp	present (0)	present (0)	present (0)	present (0)	present (0)	present (0)
69. p2 occlusal shape	elongated (1)	round (0)	round (0)	elongated (1)	round (0)	elongated (1)
70. p4 occlusal shape	elongated (1)	round (0)	round (0)	elongated (1)	round (0)	round (0)
71. m1/m2 morphology	similar-trigonid open (0)	similar-trigonid compressed (1)	similar-trigonid compressed (1)	different (2)	similar-trigonid compressed (1)	similar-trigonid compressed (1)
72. m1 trigonid	open ling. (0)	compressed (1)	compressed (1)	open ling. (0)	compressed (1)	compressed (1)
73. m1/m1 protoconid/metaconid placement	protoconid ant. (0)	same level (2)	metaconid ant. (1)	protoconid ant. (0)	metaconid ant. (1)	metaconid ant. (1)
74. m1/m2 protocristid	post.-ling. inclined (1)	transverse (0)	ant.-ling. inclined (2)	post.-ling. inclined (1)	ant.-ling. inclined (2)	ant.-ling. inclined (2)
75. m1/m2 entoconid/metaconid	entoconid smaller (0)	equal (1)	entoconid smaller (0)	equal (1)	entoconid smaller (0)	equal (1)
76. m/m2 hypconulid	small (1)	small (1)	small (1)	small (1)	small (1)	well developed (0)
77. m1/m1 hypoconid/entoconid placement	hypoconid ant. (0)	same level (2)	same level (2)	hypoconid ant. (0)	entoconid ant. (1)	same level (2)
78. m1/m2 postcristid	post.-ling. inclined (1)	transverse (0)	transverse (0)	post.-ling. inclined (1)	ant.-ling. inclined (2)	transverse (0)
79. m1/m2 labial cingulum	thin, continuous (1)	thin, continuous (1)	thin, continuous (1)	thin, continuous (1)	thin, continuous (1)	thin, continuous (1)
80. m3 talonid	very narrow (0)	broad (2)	broad (2)	broad (2)	broad (2)	broad (2)
81. m3 entoconid	absent (1)	well developed (1)	well developed (1)	well developed (1)	well developed (1)	well developed (1)

Table 4. (Extended).

Age, location, and characters	Extant Species of Emballonuridae					
	Old World		New World			
	Taphozous melanopogon	*Coleura afra*	*Balantiopteryx plicata*	*Diclidurus albus*	*Peropteryx macrotis*	*Saccopteryx bilineata*
Age	Living	Living	Living	Living	Living	Living
Geographic distribution	India, SE Asia Philippines	Africa	N. Mexico to Costa Rica	S. Mexico to South America	S. Mexico to South America	S. Mexico to South America
Upper dentition						
82. C1 anterolingual cusp	absent (1)	present (0)	present (0)	absent (1)	present (0)	present (0)
83. C1 posterolingual cusp	absent (1)	present (0)	present (0)	absent (1)	present (0)	present (0)
84. M1 parastylar region	unreduced (0)	reduced parastyle absent (2)	reduced parastyle absent (2)	reduced parastyle present (1)	reduced parastyle present (1)	reduced parastyle present (1)
85. M1 preparacrista	weakly reduced (0)	absent (2)	absent (2)	absent (2)	short (1)	short (1)

gunnelli are discussed below in the account of the latter species.

Oligopteryx floridanus differs in many characters from the new genus and species of emballonurid *Floridopteryx poyeri*, described below from the early Miocene Thomas Farm LF. Elements shared by these two extinct emballonurid species are the M1, m1–m3, dentary, and proximal femur. Perhaps the most important difference between these two species is the presence of a small, single-rooted p3 in *O. floridanus* and the absence of a p3 in *F. poyeri*. As discussed below, all living genera in the Emballonuridae also lack a p3. The most obvious difference between these two species is that *O. floridanus* is much larger. A sample of 11 M1s of *O. floridanus* have a mean anteroposterior length of 1.80 compared to a single M1 of *F. poyeri* which has an anteroposterior length of only 0.85 mm, less than half that of the larger species. This difference in size is over-emphasized by the much shorter, truncated talon of *F. poyeri* compared to *O. floridanus* that has a well-developed, posterolingual extension of the talon. Other differences that characterize the M1 of *Floridopterx* compared to *Oligopteryx* are the well-developed parastyle, weak paracingulum, bulbous anteriorly directed mesostyle, and reduced hypocone. *Floridopteryx* shares two of these characters with *Karstopteryx*, the more prominent parastyle and reduced hypocone. See the accounts of *K. gunnelli* and *F. poyeri* for more detailed comparisons between those two species. The difference in size between *O. floridanus* and *F. poyeri* is also observed in the m1 and m2 but it is not as great as the difference in size between the M1s of these two species. The m1 and m2 (samples of these two teeth combined here) of *O. floridanus* are about 20% larger (mean from a sample of 22 m1/m2s, see Table 2), anteroposterior length, 1.75 mm; maximum transverse width (talonid), 1.32 mm, compared to two m1/m2s of *F. poyeri*, with a mean anteroposterior length of 1.46 and maximum transverse width (talonid) of 1.09 mm. Features of the m1 and m2 of *Oligopteryx* are similar to those two teeth in *Floridopteryx* but there are minor differences. In *Oligopteryx*, the talonid is comparatively narrower, the metaconid is more posteriorly placed, and the protocristid is not as sharply angled from the protoconid to the metaconid. On the m3, the metaconid is located farther anteriorly in *O. floridanus* and accordingly the postcristid forms a more obtuse angle to the long axis of the tooth, whereas in *Floridopteryx* the metaconid is farther posterior and the protocristid is at a right angle to the long axis of the tooth.

Comparisons with extinct genera of Emballonuridae from the Old World.—Dental characters of all eight extinct genera and six living genera of Emballonuridae are summarized in Table 4 and Appendix 2. *Oligopteryx* differs in a number of characters from *Tachypteron franzeni*, one of the oldest known emballonurids, from the middle Eocene Messel site in Germany. Characters of *Tachypteron* are from descriptions and illustrations in Storch et al. (2002) and Smith et al. (2012). The parastylar region of M1 in *Tachypteron* is much better developed than in *Oligopteryx*, which either lacks or has a very small parastyle and has a much reduced preparacrista. The M1 and M2 of *Tachypteron* have a transversely elongated (wider than long) occlusal outline, whereas the M1 of *Oligopteryx* has a more squarish occlusal outline and M2 is longer anteroposteriorly. M1 and M2 of *Tachypteron* lack a hypocone, whereas both teeth have a well-developed hypocone in *Oligopteryx*. Both *Oligopteryx* and *Tachypteron* have a p3, distinguishing these two genera from all living emballonurids that lack a p3. However, this tooth is much larger and better developed in *Tachypteron*, with two roots and intermediate in size between the smaller p2 and larger p4; the premolars becoming progressively larger from p2 to p4. In contrast to *Tachypteron*, the p3 in *Oligopteryx* is a tiny, single-rooted tooth that is much smaller than p2. Labial cingula are very strong on the three lower premolars and three molars in *Tachypteron* (Storch et al., 2002), much better developed than the labial cingula on the lower teeth of *Oligopteryx*.

The M1 and M2 of *Vespertiliavus*, from the Eocene of Europe and northern Africa (Barghoorn, 1977; Maitre, 2014; Ravel et al., 2016), are similar to one another in size and shape, whereas the M1 and M2 of *Oligopteryx* have distinctly different morphologies, with M1 more quadrate in occlusal outline and M2 more transversely elongated. The M1 of *Vespertiliavus* has a well-developed parastyle and preparacrista, whereas the parastylar region is greatly reduced in *Oligopteryx* with the parastyle small to absent and the preparacrista very short. The M1 and M2 of *Vespertiliavus* have a very small or incipient hypocone that lacks a distinct apex, whereas the hypocone of *Oligopteryx* is a prominent cusp separated from the protocone by a deep cleft in the postprotocrista. *Vespertiliavus* also differs from *Oligopteryx* in having a double-rooted p3 with obliquely oriented roots. *Pseudovespertiliavus* from the early to middle Eocene of Algeria (Ravel et al., 2016) is similar in most features to the upper molars of *Vespertiliavus* and thus differs similarly from *Oligopteryx* (Table 4). *Pseudovespertiliavus* further differs from *Oligopteryx* in having M1 and M2 talons rounded distally rather than pointed, in lacking a connecting ridge between postprotocrista and hypoconal crest, and in having a stronger paraloph on M1.

Sigé et al. (1994) described a new genus and species of emballonurid, *Dhofarella thaleri*, from the early Oligocene Taqah fauna in Oman on the Arabian Peninsula, and Gunnell et al. (2008) described a second, smaller species of *Dhofarella*, *D. sigei*, from a late Eocene fauna in the Fayum Depression of Egypt. Both species of *Dhofarella* are represented by small samples, including half a dozen isolated teeth of *D. thaleri* and a single mandible with m1–m3 of *D. sigei*. *Dhofarella thaleri* is much smaller than *Oligopteryx floridanus* but similar in size to *O. hamaxitos*, whereas *D. sigei* is considerably smaller than both Florida species of *Oligopteryx*. Neither species of *Dhofarella* preserves the dentary anterior to the m1, so the presence or absence of p3 in this genus cannot be determined. The M1 of *Oligopteryx* differs from that of *D. thaleri* in the more strongly reduced parastylar region, shorter preparacrista, better-developed hypocone, and prominent triangular-shaped (rather than rounded) talon basin (Sigé et al., 1994). Compared to *D. thaleri*, the m1 of *Oligopteryx* has a more lingually placed paraconid, more anteriorly placed metaconid causing the protocristid to be angled anterolingually from protoconid to metaconid (protocristid is horizontal in *D. thaleri*), and more labially inflected entocristid. Besides its larger size, *Oligopteryx* differs from *D. sigei* in the similarity of m1 and m2; the m1 in *D. sigei* is narrower than the m2, especially the trigonid, and both the paraconid and metaconid are located more anteriorly (Gunnell et al., 2008). The entocristid is strongly inflected labially in *Oligopteryx* on the lower molars, whereas the entocristid is rather straight in *D. sigei*. Gunnell et al. (2008) noted that among living emballonurids *D. sigei* is most similar to *Coleura*, the only extant emballonurine genus in Africa.

Rosina and Pickford (2019) reported a large and diverse sample of fossil bats from the middle Miocene (~12–13 Ma) Otavi Mountain karst deposits from northern Namibia in southwestern Africa. Remains of emballonurids are common in the Miocene chiropteran assemblage from the Berg Aukas I site of the Otavi Mountain karst, including both taphozoines and emballonurines (Rosina and Pickford, 2020). A small species of emballonurid from the Berg Aukas I site in Namibia was recently described as a new genus and species in the subfamily Emballonurinae, *Afrillonura namibensis* (Rosina and Pickford, 2021). The M1 of *Afrillonura* is considerably smaller (length, 1.40 mm; width, 1.80 mm) than the M1 of *Oligopteryx floridanus* (mean of 11 M1s: length, 1.80 mm; width, 2.38 mm), but is similar in size to *O. hamaxitos* (M1 paratype: length, 1.37 mm; width, 1.65 mm). The most notable difference between the M1s of *Afrillonura* and *Oligopteryx* is that *Afrillonura* has a prominent rounded cusp or process at the anterolabial margin of the tooth lacking in *Oligopteryx*. We identify this cusp as the parastyle in our descriptions of emballonurid M1s, whereas Rosina and Pickford (2021, p. 6) identify this feature as a “pronounced cingulum expansion” where the ectoloph meets the precingulum (= paracingulum in our descriptions) at the anterobuccal (= anterolabial) margin of the M1. Other differences between the M1s of these two genera are the presence of a distinct metaloph, larger, more bulbous and more labial position of the metastyle, longer postmetacrista, and deeper V-shaped indentation in the metafossa in *Afrillonura*.

Differences in the lower dentition include the more elongated p2 and p4 in *Oligopteryx* compared to *Afrillonura* in which these two premolars are shorter and have a more rounded occlusal outline and a better developed talonid on p4 in *Oligopteryx*.

Comparisons with living genera of Emballonuridae.—*Oligopteryx floridanus* is similar in size to several living species in the Old World genera *Taphozous* and *Saccolaimus* (subfamily Taphozoinae), especially *Taphozous melanopogon*, but differs from taphozoines in many dental characters. The M1 and M2 of *Taphozous* and *Saccolaimus* are squarish in occlusal outline, but are more rectangular in *Oligopteryx*, especially the M2, shorter anteroposteriorly and wider transversely. Taphozoines have a well-developed parastyle and preparacrista on M1, unlike *Oligopteryx* in which the parastylar region of M1 is greatly reduced, with the preparacrista shorter and the parastyle is small to absent. *Taphozous* and *Saccolaimus* lack a paracingulum and a distinct hypocone on M1 and M2; both features are well developed in *Oligopteryx*. The M3 is more reduced in taphozoines compared to *Oligopteryx* and to living New World emballonurines, consisting only of a small portion of the ectoloph including the parastyle, preparacrista, and paracone and with a greatly reduced trigon basin and weak to absent protocone. The M3 of *Oligopteryx* is not nearly so reduced, with a postparacrista, mesostyle, premetacrista, and metacone, lacking only the postmetacrista and metastyle on the ectoloph.

In *Taphozous* and *Saccolaimus*, the lower molars are more elongated than in *Oligopteryx*, especially the m1, the paraconid and metaconid are well separated resulting from a lack of compression of the trigonid, and the metaconid is positioned posterior to the protoconid, rather than anterior to the protoconid as in *Oligopteryx*. The protocristid on the m1 and m2 of taphozoines is perpendicular to the long axis of the tooth or may be directed slightly posteriorly from the protoconid to the metaconid, whereas in *Oligopteryx* the protocristid is directed noticeably anteriorly from the protoconid to more anteriorly placed metaconid. In taphozoines, the talonid is slightly broader than the trigonid on m1 and m2 and very narrow and reduced on m3. In *Oligopterx*, the talonid is much broader than the trigonid on m1 and m2, and on m3 the talonid is not nearly so reduced as in taphozoines, only slightly narrower than the trigonid. The taphozoines have a straight entocristid on the lower molars that is not as high and lacks the deep, labially oriented, V-shaped notch found in *Oligopteryx*.

The differences in both the upper and lower molars between *Oligopteryx* and the living genera of taphozoines *Taphozous* and *Saccolaimus* are also observed in teeth of these two genera reported from several Late Cenozoic fossil sites in Africa and one in Australia. Two extinct species of *Saccolaimus* have been described from Kenya: *S. incognita* from the early Miocene Koru fauna is known from a poorly preserved partial skull with broken P4 and M2 (Butler and Hopwood, 1957) and *S. kenyensis* from the early Pliocene Kanapoi fauna in the Turkana basin, which is known from a single M1 (Gunnell and Manthi, 2020). The M1 of *Saccolaimus kenyensis* differs from that of *Oligopteryx* in the longer preparacrista, poorly developed paracingulum, crestiform and posteriorly elongated mesostyle, and short postprotocrista (Gunnell and Manthi, 2020). M1s from the middle Miocene Berg Aukas 1 site in Namibia referred to both *Saccolaimus* and *Taphozous* differ from *Oligopteryx* in their unreduced parastylar regions, prominent parastyle, longer preparacrista, nearly straight ectoloph lacking indentations in the parafossa and metafossa, lack of a hypocone, and broadly rounded talon basin (Rosina and Pickford, 2020). An M3 of *Saccolaimus* from Berg Aukas 1 has a much more reduced M3 than *Oligopteryx*, lacking the postparacrista, premetacrista, and metacone. A mandible of *Saccolaimus* from Berg Aukas 1 differs from *Oligopteryx* in lacking a p3, having the m1 trigonid more elongated with the paraconid and metaconid more widely separated, the m1 and m2 with a straight entocristid, and the m3 with a greatly reduced, narrow talonid (Rosina and Pickford, 2020).

Both extant taphozoine genera, *Taphozous* and *Saccolaimus*, have been identified from the early Pleistocene Rackham's Roost Site at the Riversleigh World Heritage Area in Australia (King et al., 2020). Several M1s from Rackham's Roost were referred to the living Australian species *Taphozous georgianus*, differing from *Oligopteryx* in the better developed parastylar region, including the presence of a parastyle and longer preparacrista, absence of a hypocone, and rounded posterior margin of the talon basin (King et al., 2020). Several fossil mandibles of *T. georgianus* from Rackham's Roost differ from *Oligopteryx* in lacking a p3 and having the m1 with a more elongated trigonid, a greater separation between the paraconid and metaconid, and metaconid located posterior to the protoconid, and a very narrow talond on m3. A single M2 referred to *Saccolaimus* from Rackham's Roost differs from the M2 of *Oligopteryx* in the squarish overall shape, lack of a well-developed 'hooked' parastyle, lack of a hypocone, and rounded posterior margin of the talon basin.

Oligopteryx floridanus is larger than any living species in the Old World emballonurine genera *Coleura*, *Emballonura*, *Mosia,* and *Paremballonura*. Although these four genera differ from *Oligopteryx* in a number of dental characters, they are more similar to the Florida genus than are *Taphozous* and *Saccolaimus*, supporting the basic dichotomy within the Emballonuridae between the Taphozoinae and Emballonurinae. Like *Oligopteryx* but unlike taphozoines, the Old World emballonurines have a reduced parastylar region on M1. Compared to *Oligopteryx*, the Old World emballonurines have a better-developed parastylar shelf labial to the paracone and a much stronger parastyle at the anterolabial termination of the paracingulum but lack a preparacrista (the ectoloph ends abruptly at the paracone). The M1 and M2 of the Old World emballonurines are more squarish in occlusal outline and the trigon basin is compressed transversely. The M1 and M2 are transversely broader in *Oligopteryx*, primarily because of the broader trigon basin. The Old World emballonurines have a distinct hypocone, but it is smaller and has a shallower notch in the postprotocrista separating it from the protocone than *Oligopteryx*. The lower premolars (p2 and p4, p3 is absent) in the Old World emballonurines are more rounded in occlusal outline, whereas the premolars are laterally compressed, elongated and blade-like in *Oligopteryx*. The trigonid on the lower m1 and m2 is not as anteroposteriorly compressed in *Coleura*, *Emballonura*, *Mosia*, and *Paremballonura* as it is in *Oligopteryx*. The Old World emballonurines have a deeper anterior portion of the dentary and lack the triangular-shaped flange extending posteriorly from the mandibular symphysis. With the exception of Pleistocene records of *Coleura* from Ethiopia and *Paremballonura* from Madagascar (Rosina and Pickford, 2021), the only other fossil record of a living genus of emballonurine from Africa is a lower m1 described as the extinct species *Coleura muthokai* from the late Pliocene of Ethiopia (Wesselman, 1984). Like the living species *C. afra*, the trigonid of m1 in *C. muthokai* is not as anterposteriorly compressed as in *Oligopteryx*.

There is considerable dental variation among the eight genera of New World emballonurids in the monophyletic subfamily Diclidurinae. We compared each of the modern genera in this group to *Oligopteryx*; first to genera in the subtribe Diclidurina (*Balantiopteryx*, *Cormura*, *Cyttarops*, *Diclidurus*, and *Peropteryx*) and then genera in the subfamily Saccopterygina (*Centronycteris*, *Rhynchonycteris*, and *Saccopteryx*). Characters for four of these genera, *Balantiopteryx*, *Diclidurus*, *Peropteryx*, and *Saccopteryx*, are included in Table 4. The dental and mandibular features discussed for each genus are only those characters that differ from *Oligopteryx*. In addition to their overall smaller size, especially when compared to *Oligopteryx floridanus*, most living New World emballonurids differ from *Oligopteryx* in having: the labial margins of the ectoloph on the upper molars with deep V-shaped notches (ectoflexi) in the the parafossa labial to the paracone and the metafossa labial to the metacone; thin, high, and sharp cristae; deeply concave or pocketed trigon and talon basins with well-defined edges; and in lacking p3.

Both living species of *Balantiopteryx* are smaller than *Oligopteryx floridanus*, whereas *B. plicata* is similar in size to the smaller species, *O. hamaxitos*. On M1 and M2, *Balantiopteryx* has a distinct paraloph and metaloph, *O. floridanus* has a weak paraloph and lacks a metaloph, and *O. hamaxitos* has a paraloph and metaloph. The M1 of *Balantiopteryx* is squarish with a narrow trigon basin compared to *Oligopteryx* which is wider transversely with a broad trigon basin. The talon on M1 in *Balantiopteryx* is shorter, more rounded, and lacks the triangular-shaped, posterolingual extension typical of *Oligopteryx.* The p2 and p4 are comparatively smaller and more rounded in occlusal outline in *Balantiopteryx* compared to the larger, laterally compressed lower premolars of *Oligopteryx*. The mandibular symphysis of *Balantiopteryx* is broader anteriorly and the mandibular flange extending posteriorly from the symphysis is weaker.

The only species of *Cormura*, *C. brevirostris*, is intermediate in size between the two species of *Oligopteryx*. The upper molars of *Cormura* and *Oligopteryx* are similar in certain characters; in both genera the parastylar region of M1 is reduced, with a tiny preparacrista that curves posteriorly, paralleling the postparacrista. *Cormura* differs from *Oligopteryx* in having M1 and M2 with a weak to absent hypocone lacking a notch in the postprotocrista separating it from the protocone, and a rounded talon on M1 that lacks a posterolingual expansion. Compared to *Oligopteryx*, the p2 and p4 of *Cormura* are rounded in occlusal outline, the paraconid and metaconid on m1/m2 are located farther apart, the entocristid is less blade-like and not as sharply inflected labially, and the mandibular flange below p4 is weaker.

Cyttarops alecto, the only species in this genus, is similar in most of its dental features to *Diclidurus*. Compared to *Oligopteryx*, the M1 of *Cyttarops* has an anteriorly oriented preparacrista and lacks a prominent, triangular posterolabial extension of the talon. *Cyttarops* differs from *Oligopteryx* in having small and rounded p2 and p4, the lower molars with the paraconid and metaconid widely separated, especially on m1, and the metaconid located posterior to the protoconid such that the protocristid is directed posterolingually from the protoconid to the metaconid.

Diclidurus contains the largest living species of New World emballonurids. The largest species, *D. ingens*, is similar in size to *Oligopteryx floridanus*; all species of *Diclidurus* are larger than *O. hamaxitos*. On M1 of *Diclidurus*, the parastylar shelf is better developed than in *Oligopteryx*, the preparacrista is anteriorly oriented, a small but distinct parastyle is present, and the talon is rounded and lacks a posterolingual expansion. The hypocone on M1 and M2 of *Diclidurus* is smaller and is separated from the protocone by a weaker notch in the postprotocrista. Similar to *Oligopteryx*, the lower premolars of *Diclidurus* are transversely flattened and blade-like, but the p2 is relatively smaller in *Diclidurus* and the p4 has a prominent posterolabial cusp that is absent in *Oligopteryx*. The m1 and m2 of *Diclidurus* are more elongated, especially m1, the paraconid and metaconid are well-separated, and the metaconid is posterior to the protoconid. The mandibular symphysis of *Diclidurus* is narrow anteriorly and has a tubercle at its posterior terminus.

Compared to *Oligopteryx*, the parastylar shelf, parastyle, and preparacrista of M1 are better developed in *Peropteryx*, and the talon is squared off and lacks a triangular, posterolingual expansionThe p2 and p4 of *Peropteryx* are rounded, not narrow and blade-like as in *Oligopteryx*. The metaconid in *Peropteryx* occupies an even more anterior position on m1 and m2 than in *Oligopteryx*, and the protocristid forms an even more oblique angle to the tooth, oriented anterolingually from the protoconid to the metaconid. The mandibular symphysis of *Peropteryx* is typical for emballonurids, with minimal anterior narrowing and a small posterior flange.

Compared to *Oligopteryx*, the M1 and M2 of *Centronycteris* have the ecotoloph on the labial margin deeply emarginated labial to the paracone (parafossa) and metacone (metafossa), a distinct metaloph, and a tall and sharp hypocone. A metaloph is present on the M1 and M2 in *O. hamaxitos*. On the M1 of *Centronycteris*, the preparacrista is labially oriented and a parastyle is present, whereas the preparacrista is posteriorly oriented and the parastyle is absent or tiny in *Oligopteryx*. The p2 and p4 of *Centronycteris* are rounded in occlusal outline, not flattened and blade-like as in *Oligopteryx*. The trigonids are compressed on the m1 and m2 in *Centronycteris* and the paraconid and metaconid are very close to one another, as close or even closer than in *Oligopteryx*. The mandibular ramus is very slender in *Centronycteris*, the symphysis is not shallower anteriorly, and there is a small flange extending posteriorly from the symphysis.

Rhynchonycteris is tiny, much smaller than either species of *Oligopteryx*. Compared to *Oligopteryx*, the crests and cusps on the ectoloph of the upper molars are tall, sharp, and blade-like in *Rhynchonycteris*, the ectoloph along the labial margins of M1 and M2 is deeply notched labial to the paracone and metacone, the hypocone is particularly tall and sharp, and the M1 has a large parastyle. On the lower m1 and m2 of *Rhynchonycteris*, the trigonid is compressed and the paraconid and metaconid are placed even closer together than in *Oligopteryx*. The horizontal ramus of the mandible in *Rhynchonycteris* is very slender and the symphysis is relatively deep anteriorly.

Compared to *Oligopteryx*, the M1 of *Saccopteryx* has a better developed parastylar shelf and parastyle and the talon lacks a posterolingual expansion, the ectoloph on the M2 has deep, V-shaped emarginations in the parafossa and metafossa, and the paraloph and metaloph on the upper molars are distinct. A metaloph absent on M1 and M2 in *O. floridanus*, present in *O. hamaxitos*. The p2 of *Saccopteryx* is compressed and blade-like, the p4 is rounded; both premolars are comparatively smaller than in *Oligopteryx*. The paraconid and metaconid on m1 and m2 are slightly farther apart in *Saccopteryx* than in *Oligopteryx* and the protocristid is nearly horizontal to the long axis of the tooth. The entocristid is U-shaped in *Saccopteryx*, not as high and sharply V-shaped as in *Oligopteryx*. The mandibular symphysis of *Saccopteryx* is deeper anteriorly and has a small posterior flange.

Remarks on Systematic Relationships.–According to Barghoorn (1977), a reduced parastylar region on M1 is one of the derived characters uniting the four genera of Old World emballonurines (tribe Emballonurini), *Coleura*, *Emballonura*, *Mosia*, *Paremballonura*, and all New World members of the family (tribe Dicliurini), and together comprising the subfamily Emballonurinae and separating them from *Taphozous* and *Saccolaimus* (subfamily Taphozoinae). *Oligopteryx floridanus* is similar to emballonurines in the strongly reduced parastylar region on M1. Most genera of smaller emballonurids have some expression of a metaloph running lingually from the base of the metacone towards the protocone, thus separating the deeply concave trigon and talon basins. According to Barghoorn (1977), the presence of a metaloph dividing the trigon and talon basins on the M1 and M2 is a primitive character. One of the most significant dental differences between the two species of *Oligopteryx* is in the development of the paraloph and metaloph on the M1 and M2. *O. floridanus* has a weak paraloph and lacks a metaloph on these two teeth compared to *O. hamaxitos*, which has both the paraloph and metaloph well developed. *Karstoptyerx gunnelli* lacks both a paraloph and metaloph on the only known M1. The hypocone has two distinct forms in the Emballonuridae. In the Emballonurinae, as well as *Oligopteryx*, the hypocone forms a distinct cusp at the termination of the postprotocrista. *Taphozous*, *Saccolaimus*, and *Vespertiliavus* do not exhibit the distinct apex of the hypocone, a derived feature according to Barghoorn (1977).

***OLIGOPTERYX HAMAXITOS* new species**

Fig. 11-15

Holotype.—UF 157768, left dentary fragment with m1-m2. Brooksville 2 Local Fauna, late Oligocene (late early Arikareean), Florida.

Paratypes.—UF 182808, right M1; UF 157786, right M2; UF 182792, distal end of humerus; UF 179983, proximal end of radius. All paratypes are from the Brooksville 2, LF, Florida.

Referred Specimens.—Brooksville 2 Local Fauna.– UF 182880, right C1; UF 182911, right P4; UF 157774, right M2; UF 182803, left c1; UF 182817, 182869, left m1/m2 (2); UF 179936, proximal humerus; UF 179909, distal humerus; UF 179914, 179915, proximal radius (2); UF 179977, distal radius. MNI is 2 based on two left m1. NISP is 15.

I-75 Local Fauna.—UF 121715, right C1; UF 16861, 121716, left C1 (2); UF 121714, left distal humerus. MNI is 2 based on two left upper canines (C1). NISP is 4.

Type Locality and Age.—Brooksville 2 Local Fauna, Hernando County, Florida, late early Arikareean (Ar2), late Oligocene.

Occurrence.–Known only from the early Oligocene (Whitneyan) I-75 LF, Alachua County, Florida and the late Oligocene (early Arikareean) Brooksville 2 LF, Hernando County, Florida.

Etymology.—*hamaxitos* (Greek), road, highway; in reference to the original discovery of this species during the construction of Interstate Highway 75.

Diagnosis.—*Oligopteryx hamaxitos* is very similar to *Oligopteryx floridanus* in most morphological characters (see generic diagnosis above), and is separated from the latter species primarily by its much smaller size. *O. hamaxitos* can also be distinguished from *O. floridanus* by the presence of a metaloph on M1 and M2. *O. hamaxitos* can be separated from *Karstopteryx gunnelli* by its smaller size, lack of a parastyle, and larger hypocone separated from the protocone by a distinct notch in the postprotocrista. *Oligopteryx hamaxitos* can be separated from all other emballonurids by the following combination of characters. M1 with parastyle reduced to absent, preparacrista very short, well-developed paracingulum, talon triangular in shape with prominent posterolingual extension; M1 and M2 labial margin of metafossa with shallow V-shaped indentation labial to metacone, deep V-shaped notch in postprotocrista separating protocone and hypocone, hypocone distinct and triangular-shaped, talon basin deeply concave and separated from metacingulum by distinct notch just posterior and lingual to base of metacone; M2 with well-developed hooked parastyle at anterolabial termination of paracingulum, shallow V-shaped indentation in labial margin of parafossa; m1 and m2 nyctalodont, talonid significantly broader and slightly longer than trigonid, trigonid compressed with paraconid and metaconid located close together along lingual margin, metaconid anterior to protoconid, protocristid at angle to long axis of toothrow, entocristid blade-like and distinctly V-shaped with apex oriented labially and open lingually; dentary with triangular-shaped process projecting ventrally below p4.

Morphological Descriptions

Oligopteryx hamaxitos from the Brooksville 2 and I-75 local faunas is much rarer than the larger *O. floridanus* from these same two sites. There are only 15 specimens of *O. hamaxitos*, 11 from Brooksville 2 (MNI of 2) and 4 from I-75 (MNI of 2). Several teeth present in *O. floridanus* are not represented in the sample of *O. hamaxitos*, including all lower premolars and M3/m3. There is a large enough sample to confirm that *O. hamaxitos* represents a distinct species, very closely related to *O. floridanus*. The following descriptions and comparisons are not as detailed as those for *O. floridanu*s because so many of the dental features are identical between the two species, except for the smaller size of *O. hamaxitos*. The M1 and m1 lengths and humeral midshaft diameter (Tables 1, 2) provide estimates of its body weight ranging from 7.3 to 11.7 g (by method of Gunnell et al., 2009). The comparisons above of *O. floridanus* with other fossil and modern emballonurids are at the generic level, and therefore differences from *O. floridanus* also pertain to *O. hamaxitos*.

Upper dentition.–Compared to *Oligopteryx floridanus*, the only upper tooth position not represented in the sample of *O. hamaxitos* is the M3. There is a single M1 of *O. hamaxitos* from Brooksville 2 (UF 182808, paratype; Fig. 11 C-D). The M1 of *O. hamaxitos* is very similar in overall morphology to the large sample of M1s of *O. floridanus* from Brooksville. The parastylar region anterior and labial to the paracone is highly reduced. A parastyle is absent and the preparacrista is extremely short, consisting of a barely discernible ridge, oriented labially from the paracone. The paracingulum (= precingulum) is well developed, with a slight convex bulge, not a cusp, at its anterolabial termination. There is a very shallow, V-shaped emargination in the metafossa along the ectoloph on the labial margin. The paracone and metacone are oriented vertically, the protocone has an anterior orientation. The low, rounded protocone is located on the anterolingual margin. There is a shallow notch in the postprotocrista, about two thirds of the distance between the protocone and hypocone, isolating the low, rounded hypocone. The hypocone is lingual to the protocone and posterior to the metacone. A paraloph and metaloph are well-developed. The metaloph separates the trigon and talon basins. The trigon basin is concave but rather shallow compared to other New World emballonurids. The talon basin is much deeper and better defined, being deepest posterior and lingual to the metacone. The prominent, triangular-shaped talon forms the posterolingual extension of the M1. The talon extends farther posteriorly than the metacingulum and is separated from it by a distinct V-shaped notch posterior to the base of the metacone. The narrow metacingulum (= postcingulum) extends from the base of the metacone to the metastyle.

There are two M2s of *Oligopteryx hamaxitos* from Brooksville 2. UF 157786 (paratype; Fig. 11 A-B) is a complete tooth, UF 157774 is broken in half and lacks the apex of the metacone. The following description focuses on the differences between the M2 and M1. Characters not listed are identical to the M1 described in the previous paragraph. The two M2s of *O. hamaxitos* are very similar, except for smaller size, to the larger sample of M2s of *O. floridanus* from Brooksville 2. One important difference is the presence in *O. hamaxitos* of a well-developed metaloph on the M2, extending anterolingually from the base of the metacone ending before reaching the postprotocrista and separating the trigon and talon basins. A metaloph is absent on the M2 in *O. floridanus*. A well-developed paraloph is present on the M2 in *O. hamaxitos*, extending from the base of the paracone to the base of the protocone. *O. floridanus* also has a fairly well-developed paraloph on M2. The parastylar region of M2 in *O. hamaxitos* is much better developed than on the M1. There is a strong, curved parastyle that forms the anterolabial corner of the tooth. The parastyle is located at the anterolabial termination of the well-developed paracingulum. The preparacrista is complete, connecting the paracone to the parastyle. The ectoloph on the labial margin has shallow, sharply V-shaped notches in the parafossa labial to the paracone and metafossa labial to the metacone. The metacone is slightly taller than the paracone, the protocone is much lower. There is a deep, V-shaped notch in the postprotocrista, about halfway between the protocone and the well-developed hypocone. This notch is also present in the M1 but is not as prominent. The hypocone is a distinct, sharply pointed cusp about half the height of, and well lingual to, the protocone. The elliptical trigon basin is concave but shallow for an emballonurid. The talon basin is more rounded and much deeper, deepest posterior and lingual to the posterior base of the metacone. The talon basin extends farther posteriorly than the metacingulum and is separated from it by a shallow indentation that is not as prominent as the deep, V-shaped notch on M1. The talon is more rounded than on M1 and does not extend as far lingually. The metacingulum is narrow and indistinct.

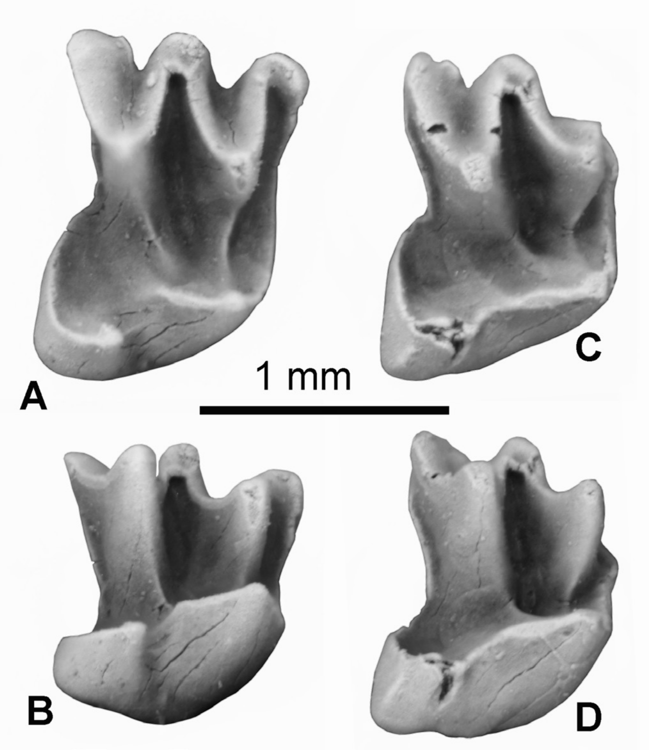

Figure 11. Right upper molars of *Oligopteryx hamaxitos* from Brooksville 2 LF. A-B, UF 157786, M2, in occlusal (A) and lingual (B) views; C-D, UF 182808, M1, in occlusal (C) and lingual (D) views.

There is one upper canine (C1) of *Oligop-*

teryx hamaxitos from Brooksville 2 (UF 182880; Fig. 12A-C). There are three C1s of a small emballonurid from I-75, the most abundant element of *O. hamaxitos* in this fauna. These canines are laterally compressed and lack an internal (lingual) cingulum. Basal cingula are almost entirely lacking. They have prominent anterior and posterior secondary cusps that are similar in size. The cusps are located on the anterolingual and posterolingual margins of the canines, respectively. No smaller cusps are present. These canines are similar to those of other emballonurids in overall shape (rounded or convex on the labial surface and flattened on the lingual surface) and possession of prominent spike-like anterior and posterior secondary cusps. In cross-section the canines form a hemicircle with the convex portion labial. The fossils differ from modern emballonurids in the total lack of an internal cingulum, lack of tiny secondary cusps, and a more triangular shape. These upper canines are smaller than those of *O. floridanus* described above, with a lesser angle between the root and crown, weaker lingual cingulum, and more distinct anterior secondary cusp.

The only other upper tooth locus represented in our sample of *Oligopteryx hamaxitos* is a P4 (UF 182911; Fig. 13) from the Brooksville 2 LF. The P4 of *O. hamaxitos* is similar to two P4s assigned to *O. floridanus* (Fig. 6), except for its smaller overall size and relatively smaller talon. In labial and lingual views, the central cusp or protocone of the P4 is tall, narrow, and sharply triangular, almost caniniform in shape. The anterior margin is nearly vertical, whereas the posterior margin is more gently curved. Prominent basal cusps are present at the anterolingual and posterolabial margins. The anterolingual cusp is slightly smaller, triangular, and in a more ventral position whereas the posterolabial cusp is larger, more rounded, and located dorsal to the anterolingual cusp. In occlusal view, the protocone is rounded, especially anteriorly, and descends along its anterior margin almost vertically to the anterolingual cusp. Posteriorly, the protocone is connected to a narrow, blade-like crest that terminates at the posterolabial cusp. The P4 has a small lingual lobe or talon with a shallow talon basin surrounded by a cingulum. The anterior cingulum surrounding the base of the protocone is separated from the talon by an anterolingual notch, with anterolingual cingular cusps on either side of

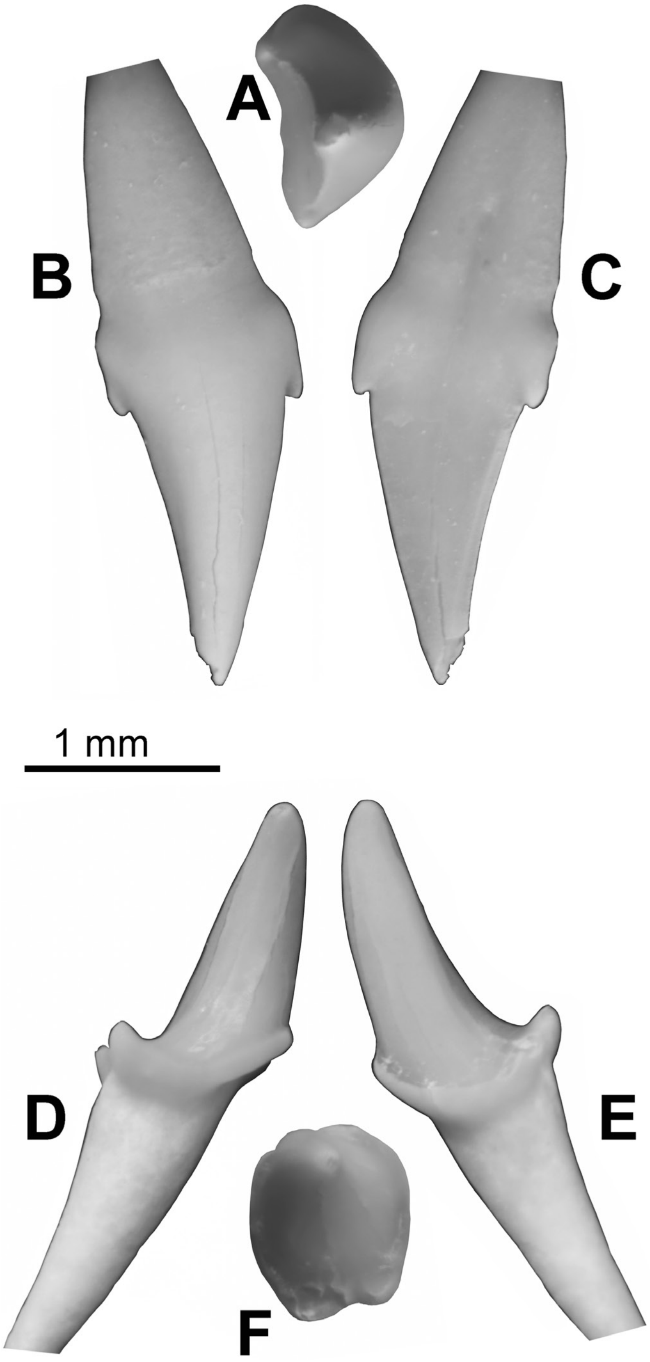

Figure 12. Canines referred to *Oligopteryx hamaxitos* from Brooksville 2 LF. A-C, UF 182880, right C1 in occlusal (A), labial (B), and lingual (C) views. D-F, UF 182803, left c1 in lingual (D), labial (E), and occlusal (F) views.

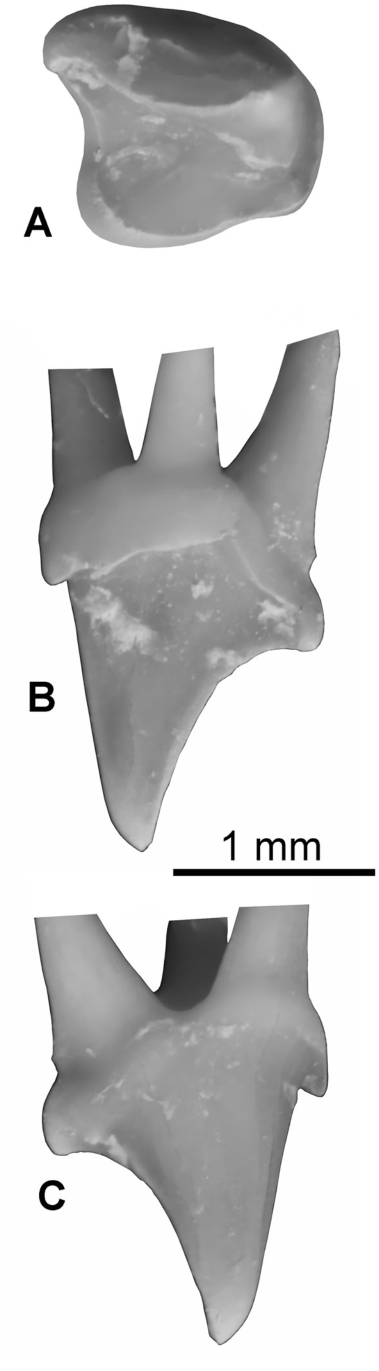

Figure 13. Right P4 referred to *Oligopteryx hamaxitos* from Brooksville 2 LF. UF 182911, right P4 in occlusal (A), lingual (B), and labial (C) views.

the notch. The well-developed lingual cingulum descends gently from the anterolingual cusp to the posterior edge of the talon and is confluent with a posterior cingulum that ascends at a sharper angle from a notch at the posterior edge of the talon to the posterolabial cusp. In occlusal view, the posterior cingulum curves gently anterior labial to the talon and then curves back posteriorly to the posterolabial cusp A labial cingulum is absent. The P4 is three-rooted, with one root each ventral to the protocone, posterolabial crest, and talon.

Lower dentition.—Among the tooth positions in the lower dentition, only the m1, m2, and canine (c1) are represented in the sample of *Oligopteryx hamaxitos* from Brooksville 2. There are no lower teeth of *O. hamaxitos* from I-75. The type specimen of *O. hamaxitos* (UF 157768; Fig. 14) is a partial left dentary with the m1 and m2, as well as the alveolus for the posterior root of p4 and alveoli for both roots of m3. The m1 and m2 are very similar in morphology, and when they occur as isolated teeth cannot be reliably separated. Therefore, the following description applies to both the m1 and m2 and is based primarily on UF 157768 (Fig. 14), together with data on dental variation from two additional isolated m1/m2s from Brooksvile 2 (UF 182817, 182869). Measurements of the m1 and m2 of *O. hamaxitos* are presented in Table 2. The talonid is broader than the trigonid on both m1 and m2. Because of the anteroposterior compression of the trigonid, the talonid is also slightly longer than the trigonid. Both teeth are nyctalodont, the postcristid connects the hypoconid and the much smaller hypoconulid. The paraconid and metaconid are located close together along the lingual margin. The metaconid is located anterior to the protoconid and thus the protocristid is oriented at an angle to the long axis of the tooth row, extending from the more posterior protoconid anterolingually to the more anterior metaconid. The four lingual cusps are rather low, the metaconid is the tallest, followed by the entoconid and paraconid, with the much smaller hypoconulid lowest. The metaconid and entoconid are vertical, the paraconid is oriented slightly anteriorly. The labial cusps are taller than the lingual cusps, with the protoconid the tallest cusp on the m1 and m2, followed by the hypoconid. The cristid obliqua meets the trigonid at the lingual base of the protoconid. The high, sharp, angular entocristid has a distinct notch about halfway between the metaconid and entoconid. The apex of

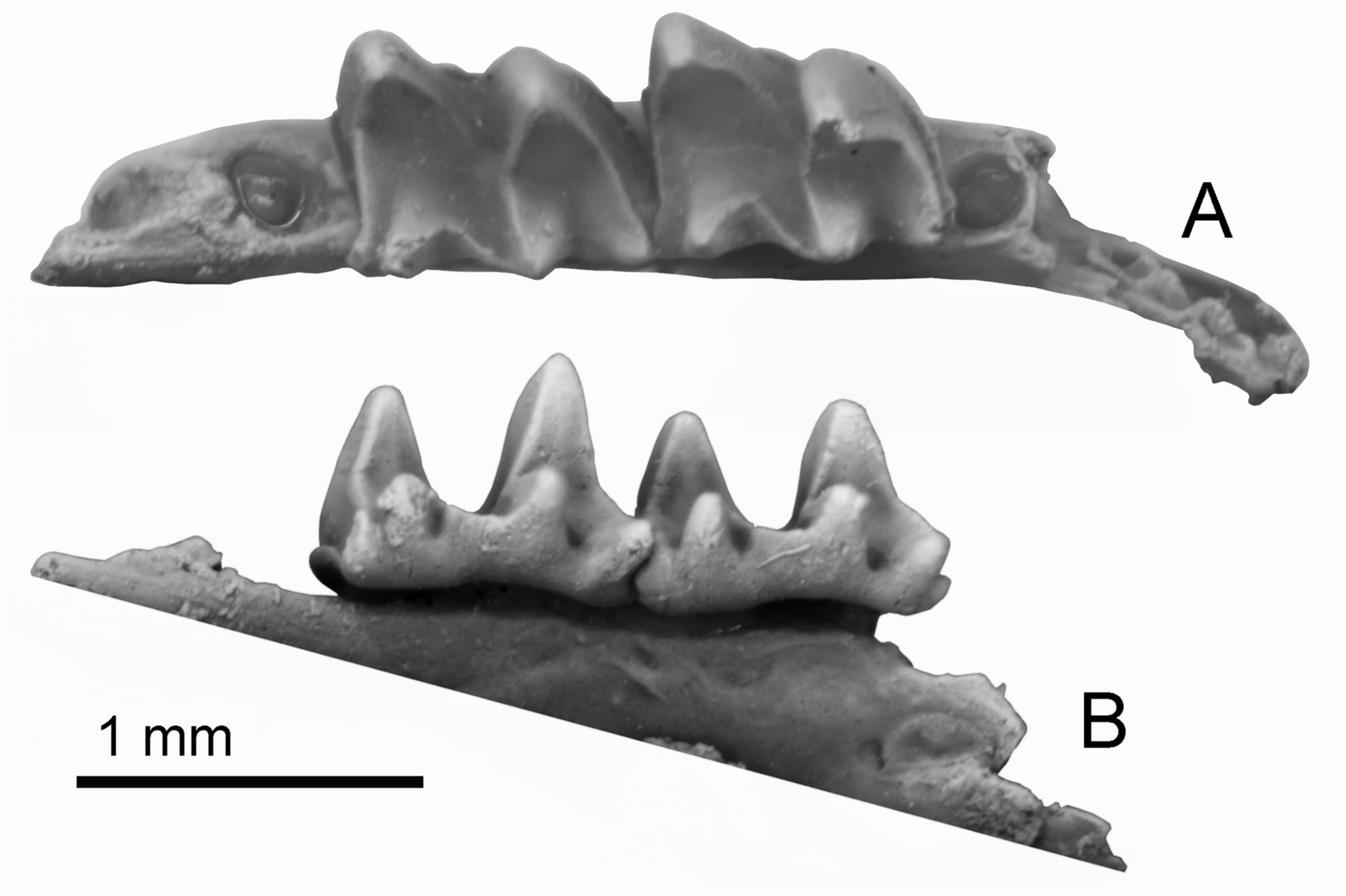

Figure 14. Mandible of *Oligopteryx hamaxitos* from Brooksville 2 LF. UF 157768 (holotype), left dentary fragment with m1-m2 in occlusal (A) and lingual (B) views.

the notch in the entocristid is oriented labially and is open lingually. The entocristid on the m1 of the type mandible penetrates somewhat more deeply into the talonid basin than does the entocristid on m2 on this same specimen. The small hypoconulid is located at the posterolingual corner of the tooth and is separated from the much larger entoconid immediately anterior on the lingual margin by a distinct notch or groove. The labial cingulum extends from the paraconid to the hypoconid, but is weak compared to other emballonurids, especially labial to the protoconid and hypoconid. The labial cingulum is stronger on one of the isolated lower molars (UF 182869), than on the type. The anterior cingulum or mesial cingulum is well-developed with a small cuspid at its anterolingual termination. This cuspid is larger in the two isolated lower molars. The postcingulum or distal cingulum is weak.

The left c1 (UF 182803; Fig. 12 D-F) of *Oligopteryx hamaxitos* from the Brooksville 2 LF has a tall, slender main cusp with a narrow root. It has a less anteroposteriorly elongate and less transversely narrowed crown base than those of *O. floridanus*. It bears strong labial and lingual cingula with a prominent posterolingual secondary cusp and weaker posterolabial, anterolabial, and anterolingual cingular cusps. Between these cingular cusps, the cingulum shows an anterior indentation to accommodate the lower incisors and a posterior indentation to accommodate the p2.

Dentary.—The holotype partial dentary (UF 157768) of *Oligopteryx hamaxitos* preserves the ventral margin of the horizontal ramus from below p4 to m2. The ramus has a straight ventral margin below the two anterior molars. Ventral to the anterior alveolus of p4 there is a triangular-shaped flange that is very similar to the flange extending posteriorly from the mandibular symphysis in *O. floridanus*. No specimens in the Brooksville sample preserve the portion of the dentary that would reveal the presence (or absence) of a p3. The presence of a p3, although tiny and single-rooted, is one of the most diagnostic features of *O. floridanus*.

Humerus.—Both the proximal (UF 179936) and distal (UF 182792, paratype; 179909) ends of the humerus are represented in the sample of *Oligopteryx hamaxitos* from Brooksville 2. There is also a distal humerus from I-75 (UF 121714). Except for their much smaller size, these four specimens are very similar to proximal and distal humeri of *O. floridanus* from Brooksville 2. Measurements of the humerus and radius of *O. hamaxitos* are presented in Table 3.

The single proximal end of a humerus from Brooksville 2 referred to *Oligopteryx hamaxitos* (UF 179936) is somewhat damaged. In posterior view, the humeral head is elliptical in shape, somewhat transversely flattened, rounded distally, and more pointed or triangular proximally. The head projects farther proximally than either the greater or lesser tuberosities. The head is not in the center of the shaft but is shifted noticeably laterally, located closer to the greater tuberosity than to the lesser tuberosity. The head is oriented at a slight angle to the shaft, canted distally toward the greater tuberosity. The greater tuberosity is rather elongated, rounded at its proximal end, and oriented at about a 45° angle to the shaft. The lesser tuberosity is considerably larger than the greater tuberosity, forming a large, triangular-shaped process with a squared-off proximal end. The greater and lesser tuberosities project about the same distance proximally. In proximal view, the pointed proximal portion of the head extends anteriorly to the base of the pectoral ridge. The larger size of the lesser tuberosity compared to the greater tuberosity is even more evident when viewed proximally. The lesser tuberosity is a prominent, triangular-shaped process extending medially, with a rounded anterior edge and straight posterior edge. It is about three times larger than the greater tuberosity. In this same view, the greater tuberosity is a narrow process with rounded edges, somewhat elongated in the anteroposterior dimension, with a shallow indentation about halfway along its length. The supraglenoid fossa is very shallow. In lateral view, the pectoral ridge is rather short, broad, especially proximally, and triangular in shape. There is some variation in the shape of the pectoral ridge in the sample of proximal humeri from Brooksville 2; in most specimens this ridge is triangular but in several it is more rectangular. In medial view, the pectoral ridge bears a distinct, raised ridge that is oriented proximodistally, dividing the pectoral ridge into two approximately equal sections. There is a weak medial ridge on the shaft distal to the lesser tuberosity.

The distal articular surface of the humerus of *Oligopteryx hamaxitos* (description based on UF 121714, 179909, 182792) is slightly offset from the shaft, with the lateral ridge of the capitulum lateral to the shaft (Fig. 15). The transversely narrow but proximodistally deep lateral ridge of the capitulum is separated by a very shallow groove from the bulbous almost spherical medial ridge of the capitulum. The lateral ridge of the capitulum is the tallest portion of the distal articular surface, easily twice as high in the proximal-distal dimension as in the transverse dimension. The trochlea meets the medial ridge of the capitulum at about a 45° angle and the two facets are separated by a prominent groove. The trochlea is separated from the epitrochlea (medial epicondyle) by a deep rounded notch. The spinous process of the epitrochlea (distal spinous process) has a sharply triangular distal tip. The spinous process is somewhat less prominent than in *O. floridanus*. In medial view, the spinous process has a slightly more posterior orientation compared to *O. floridanus* in which this process is more vertical and parallel to the shaft. The radial fossa is shallow.

Radius.—The proximal end of the radius of *Oligopteryx hamaxitos* is represented by three specimens from Brooksville 2, UF 179983 (paratype) and UF 179914, 179915. The proximalmost extension of the radius has a gently rounded curvature, not triangular shaped as in most bats. The proximal articular surface consists of three slightly concave articular facets, corresponding to the three articular facets on the distal end of the humerus, the lateral

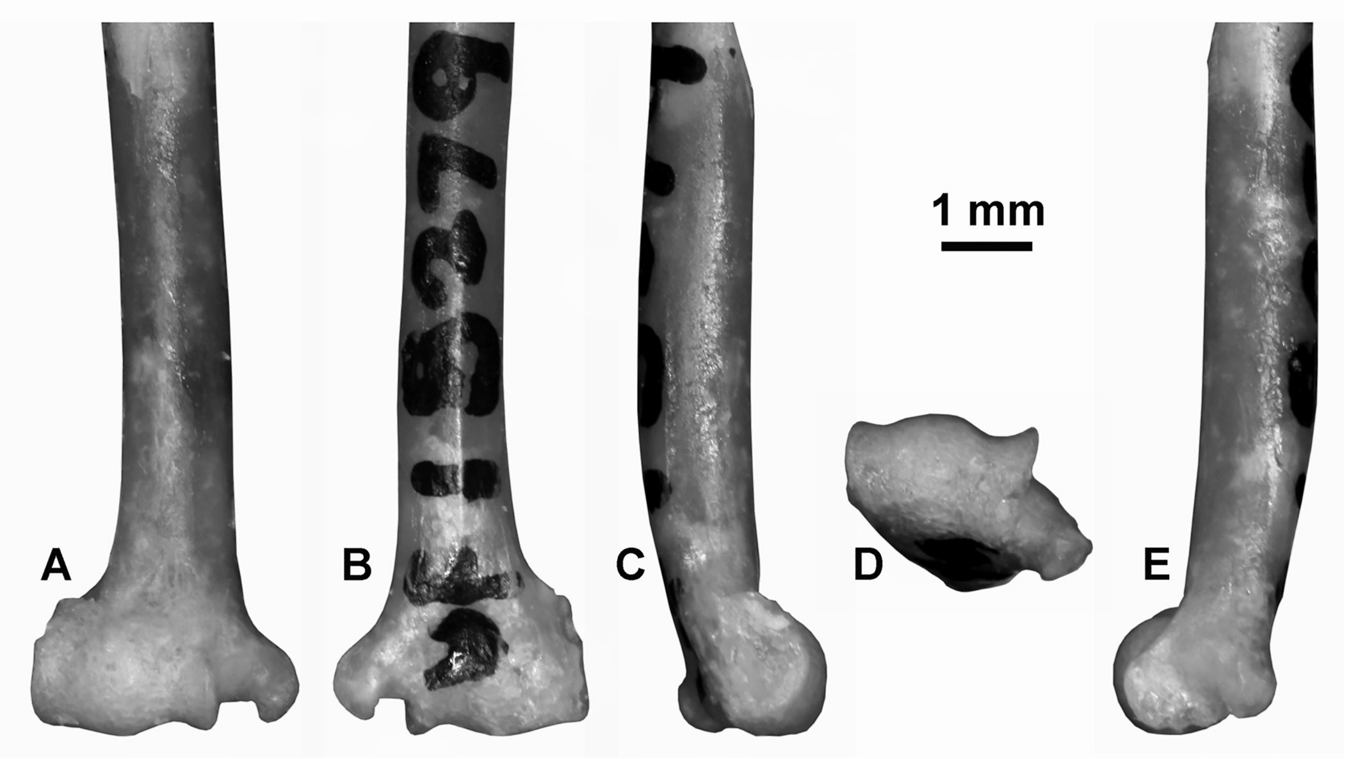

Figure 15. Distal humerus of *Oligopteryx hamaxitos* from Brooksville 2 LF. UF 182792 in anterior (A), posterior (B), lateral (C), distal (D), and medial (E) views.

and medial ridges of the capitulum and the trochlea. The facet for the medial ridge of the capitulum is a large, rounded concavity that occupies almost half of the proximal articular surface of the radius. The articular facet for the lateral ridge of the capitulum is shallower and narrower transversely but is taller or deeper in the proximodistal direction. The articular facet for the trochlea is nearly flat and consists of a narrow, medially directed process that is blunt or squared-off on its medial surface. Distal to the articular surface for the trochlea is a deep pit, the flexor fossa.

A single distal radius (UF 179977) of *Oligopteryx hamaxitos* is known from Brooksville 2. The distal end of the radius exhibits limited morphological characters. In anterior view, the distal edge of the articular surface is essentially straight, nearly horizontal to the shaft. There is a slight convexity representing the styloid process on the anterolateral edge of the articular surface. In posterior view, the distal edge of the articular surface forms a 45° angle to the shaft, trending distally from lateral to medial. The distal articular surface is deeply concave where it articulates with the lunar bone of the carpus. Just proximal to the lateral edge of the distal articular surface on the posterior surface of the shaft is a prominent, triangular-shaped, laterally oriented process that corresponds to the distalmost portion of the ulna

Comparisons with other Emballonuridae

As noted above, *Oligopteryx hamaxitos and O. floridanus* are very similar, with the primary difference between the two species being the much smaller size of *O. hamaxitos* (See comparative measurements of the teeth in Tables 1 and 2 and the humerus and radius in Table 3). Other than size, the most notable difference between these two species is the presence of a well-developed metaloph on M1 and M2 of *O. hamaxitos*. Upper M1s and M2s of *O. floridanus* generally lack the metaloph or have this character very weakly developed. In addition to their small size, the upper canines (C1) of *O. hamaxitos* differ from those of *O. floridanus* in the lesser angle between the root and crown, weaker lingual cingulum, and more distinct anterior secondary cusp. The lower canine (c1) of *O. hamaxitos* is more anteroposteriorly elongate and has a less transversely narrowed crown base than lower canines of *O. floridanus*. The spinous process on the distal end of the humerus in *O. hamaxitos* is somewhat less prominent and has a slightly more posterior orientation than in *O. floridanus*. Differences between *O. hamaxitos* and. *Karstopteryx gunnelli* from the latest Oligocene Buda LF, are the same as the characters that distinguish *K. gunnelli* from *O. floridanus*, as discussed above in the account of the latter species. In addition, *O. hamaxitos* is smaller than *K. gunnelli*, and also differs in the presence of a paraloph and metaloph on M1, both of which are absent in *K. gunnelli*. Comparisons of morphological characters of *O. floridanus* with those of all other extinct and extant genera of emballonurids (see above), including the genus *Floridopteryx* from the the early Miocene Thomas Farm LF, apply also to *O. hamaxitos*. Size comparisons of *O. hamaxitos* with other genera of emballonurids are also mentioned above under the *O. floridanus* account.

KARSTOPTERYX new genus

Type Species.—*Karstopteryx gunnelli*.

Included Species.—Only the type species is known.

Diagnosis.—All characters pertain to the holotype M1, the only tooth represented in the hypodigm of *Karstopteryx gunnelli*. The M1 has a greatly reduced anterolabial portion of the tooth, including the stylar shelf labial to the paracone, but has a well developed, rounded parastyle at the anterolabial terminus of the paracingulum. The preparacrista is very short and oriented anteriorly. A weakly concave indentation is present in the metafossa labial to the metacone, not a sharply V-shaped indentation. The metacone is taller than the paracone. The paracingulum curves posterolingually from the parastyle to the protocone. The weak hypocone is not separated from the protocone by a distinct notch in the postprotocrista. A paraloph and metaloph are absent. The trigon is triangular in shape not squarish. The talon has rounded lingual, labial, and posterior margins and lacks a deep, central pit.

Etymology.—*Karst* (German), a type of topography formed by the dissolution of limestone, forming caves, sinkholes and other solution features, and *pteryx* (Greek), wing, a common ending for generic names in the family Emballonuridae. ‘Karst’ refers to the topography that characterizes much of northern peninsular Florida, where the limestone terrain has been extensively eroded forming numerous caves, sinkholes, fissures, and other karst-derived fossil deposits that have produced bats, including not only the type locality, the Buda Quarry, but also the other three fossil localites described in this paper.

KARSTOPTERYX GUNNELLI new species

Fig. 4 G-H

Holotype.—UF 97386, right M1 (Fig. 4 G-H) Buda Local Fauna, late Oligocene (early late Arikareean), Alachua County, Florida. This species is known only from the holotype.

Type Locality and Age.—Buda Local Fauna, Buda Quarry, near Buda, about 7 km southwest of High Springs, Alachua County, Florida, early late Arikareean (Ar3), latest Oligocene.

Occurrence.—Known only by the type specimen from the type locality.

Etymology.—Named for the late Gregg F. Gunnell in honor of his many important contributions to our knowledge of Tertiary Chiroptera.

Diagnosis.—Same as for the genus.

Morphological Description

A large emballonurid is represented in the Buda LF by a single, well-preserved M1 (UF 97386; Fig. 4 G-H), here described as the new genus and species *Karstopteryx gunnelli*. This tooth is similar in size and morphology to the M1s of *Oligopteryx floridanus*, from Brooksville 2 and I-75 (Table 1), but there are several important differences. Although the anterolabial portion of the M1 of *K. gunnelli* is greatly reduced, in particular the stylar shelf labial to the paracone, preparacrista and postparacrista, there is a prominent parastyle with a rounded anterior projection at the anterolabial terminus of the paracingulum. The parastyle is at the same level as the paracone and metacone. The preparacrista is very short and anteriorly oriented. The parafossa consists of a slight indentation in the labial margin labial to the paracone and the metafossa forms a gently concave indentation labial to the metacone. The mesostyle is rounded, whereas the metastyle is narrow, compressed anteroposteriorly, and extends somewhat farther labially than the mesostyle. In lingual view, these two cusps are about the same height, with the mesostyle vertical and the metastyle oriented slightly posteriorly. The paracone and metacone are similar in size and shape in occlusal view but the paracone is considerably lower in lingual view. The paracingulum (= precingulum) curves gently posteriorly and lingually, merging with the preprotocrista, and then meeting the protocone at the same level as the paracone anteroposteriorly. The hypocone is weak and there is no V-shaped notch in the postprotocrista separating the hypocone from the protocone in lingual view. Both a paraloph and metaloph are absent. The trigon basin is rather shallow and triangular or V-shaped. The trigon and talon are separated by a low but distinct ridge that extends from the postprotocrista between the protocone and hypocone and is directed posterolabially to the posterior base of the metacone. The talon has rounded lingual, labial, and posterior margins and lacks a deep, central pit. The posterolabial margin of the talon extends farther posteriorly than the metacingulum (= postcingulum) and is separated from it by a distinct, V-shaped notch.

Comparisons with other Emballonuridae

The Buda emballonurid M1 (UF 97386), described here as *Karstopteryx gunnelli*, shares characters with the M1s of *Oligopteryx floridanus* and *O. hamaxitos* from Brooksville 2, in particular the overall reduction of the anterolabial portion of the tooth, including the stylar shelf labial to the paracone, and the greatly reduced preparacrista. However, the Buda M1 differs from the two species of *Oligopteryx* in several important features, the most obvious being the more prominent parastyle, which is larger in the Buda tooth than in all but one M1 of *O. floridanus* (UF 182787). Another difference is the anterior orientation of the tiny preparacrista in *K. gunnelli*. The preparacrista is also greatly reduced in *O. floridanus* and *O. hamaxitos* but is more posteriorly oriented and parallel to the postparacrista. The ectoflexus on the labial margin of the Buda M1 has a very slight indentation in the metafossa labial to the metacone *in K. gunnelli*, whereas the two species of *Oligopteryx* have a stronger V-shaped emargination in the metafossa of M1. In lingual view, the paracone is lower than the metacone in *K. gunnelli*, whereas these two cusps are the same height in *O. floridanus* and *O. hamaxitos*. The paracingulum curves gently posterolingually to meet the protocone in *K. gunnelli*, with the protocone located directly lingual to the paracone. In the two species of *Oligopteryx*, the paracingulum on M1 does not curve posteriorly but forms the rather straight anterior margin horizontal to the long axis of the tooth, with the protocone in a more anterior position at the anterolingual corner of the M1, slightly anterior to the paracone. The M1 of *K. gunnelli* has a very weak hypocone and lacks a distinct notch in the postprotocrista between the hypocone and protocone, whereas *O. floridanus* and *O. hamaxitos* have a more prominent hypocone and a deep V-shaped notch in the postprotocrista separating the hypocone and protocone. A paraloph and metaloph are both lacking on the M1 of *K. gunnelli*, whereas *O. hamaxitos*, has both the paraloph and metaloph well developed on this tooth, and *O. floridanus* has an intermediate condition, possessing a weak paraloph but lacking a metaloph. The trigon is somewhat smaller and triangular-shaped in *K. gunnelli*, compared to the more squarish trigon in *O. floridanus* and *O. hamaxitos*. The anterior margin of the trigon in *K. gunnelli* consists of the paracingulum that curves posterolingually from the prominent parastyle, merges with the preprotocrista, and then meets the protocone. The posterior margin of the trigon consists of a low, weak ridge that extends from the posterior base of the metacone anterolingually to meet the postprotocrista between the protocone and hypocone. The trigon is somewhat larger in *O. floridanus* and *O. hamaxitos* and squarish not triangular in shape, particularly the anterior and lingual margins. Compared to the two species of *Oligopteryx* from Brooksville 2 and I-75, the talon of *K. gunnelli* is smaller and has rounded posterior, lingual, and labial margins, with the anterolabial portion of the talon meeting the lingual end of the metacingulum posterior to the base of the metacone. In *O. floridanus* and *O. hamaxitos*, the talon of M1 is more angular and noticeably larger than in *K. gunnelli* in both the anteroposterior and labiolingual dimensions. The talon of the two species of *Oligopteryx* from Brooksville 2 and I-75 has a well-developed, triangular posterolingual projection and the posterior margin trends slightly anterolingually from the posterolingual corner to the anterolabial corner located posterior and labial to the end of the metacingulum and slightly labial to the base of the metacone. The differences between the single M1 of *K. gunnelli* and the M1s of *O. floridanus* and *O. hamaxitos* are significant and indicate this tooth represents a distinct genus and species of emballonurid.

The M1 of *Karstopteryx gunnelli* is considerably different from the M1 of *Floridopteryx poyeri*, the youngest emballonurid from the Cenozoic of Florida from the early Miocene (early Hemingfordian, He1) Thomas Farm LF (see next species account). The single M1 of *Floridopteryx* is damaged, with the posterolabial portion of the tooth missing. *F. poyeri* is a small bat, with the anteroposterior length of M1 (0.85 mm) less than half that of the much larger *K. gunnelli* (1.75 mm). Both *Karstopteryx* and *Floridopteryx* have a well-developed parastyle, although this feature is larger in the Buda M1 with a more prominent, rounded anterior projection. The labial margin and labial cusps of the M1 differ between the two species. *K. gunnelli* has a well-developed indentation in the parafossa labial to the paracone, a rather small mesostyle, and a weak indentation in the metafossa labial to the metacone, whereas *Floridopteryx* has a weak indentation in the parafossa, a large, bulbous mesostyle, and appears to have a deeper indentation in the metafossa, although the metacone, premetacrista, and labial margin of the tooth posterior to the mesostyle are damaged. The protocone is more anteriorly placed in *Floridopteryx*, at the anterolabial corner of the M1 somewhat anterior to the paracone, whereas the protocone is more posterior in *Karstopteryx* directly lingual to the paracone. A weak paraloph and metaloph are present in *Floridopteryx*, whereas these structures are absent in *Karstopteryx*. The lingual portion of the M1 is more rounded in *Karstopteryx*, especially the anterior and posterior margins, whereas the lingual half of this tooth is more squarish in *Floridopteryx*, with both the anterior and posterior margins essentially straight and tranverse to the long axis of the tooth. The talon is considerably longer in *Karstopteryx* with a rounded posterior margin, whereas the shorter talon in *Floridopteryx* is truncated posteriorly with a straight posterior margin.

Karstopteryx gunnelli differs from other extinct genera of emballonurids from the Old World and living genera of emballonurids from both the Old World and New World in almost all of the same characters as discussed above under the *Oligopteryx floridanus* account.

***FLORIDOPTERYX* new genus**

Type Species.—*Floridopteryx poyeri*.

Included Species.—Only the type species is known.

Diagnosis.—The m1/m2 are nyctalodont, the talonid is much broader than the trigonid, the talonid is also longer than the trigonid because of the anteroposterior compression of the trigonid, the paraconid and metaconid are close together along the lingual margin, the metaconid is anterior to the protoconid, the protocristid trends anterolingually from the protoconid to the metaconid, the paracristid is gently curved, the paraconid, metaconid, and entoconid are conical with rounded apices and vertically oriented, the protoconid and hypoconid are larger than the lingual cusps with sharply pointed apices, and the hypoconulid is rather large. The m3 has the trigonid broader than the talonid, the paraconid and metaconid are located close to one another along the lingual margin but both cusps are more posterior than on m1/m2, the paracristid and protocristid meet at a more acute angle than on m1/m2, the protoconid and metaconid are located at the same level and the protocristid is at a right angle to the long axis of tooth. The dentary has a long mandibular symphysis extending posteriorly to the p4 and with a rounded projection ventral to the p2 and p4, a p3 is absent, the anterior alveolus of the m1 is flattened anteroposteriorly, a large elliptical mental foramen is present ventral to the p2, a tiny mental foramen is present on the symphysis ventral to the incisor alveoli, the ascending ramus is upturned dorsally posterior to the toothrow, the coronoid process is short and slender dorsally, the angular process is at the same level as the alveolar margin of the toothrow and flares laterally, the articular process is dorsal to the alveolar margin, and the mandibular foramen is large, ventral to the toothrow, and below the tip of coronoid. The M1 has the parastylar region highly reduced anterior and labial to paracone, a well-developed parastyle is present at the anterolabial termination of the narrow paracingulum, the preparacrista very short and oriented labially, the mesostyle is bulbous and oriented anteriorly, the hypocone is small and not separated from the protocone by a notch, and the talon is squarish and somewhat truncated anteroposteriorly.

Etymology.—Named for the state of Florida and *pteryx* (Greek), wing, a common ending for generic names in the family Emballonuridae.

FLORIDOPTERYX POYERI new species
Fig. 16-19

Holotype.—UF 121132, right m1 Thomas Farm LF, early Miocene (early Hemingfordian), Gilchrist County, Florida.

Paratypes.—UF 108661, complete edentulous right mandible with alveoli for i1-m3; UF 121134, partial right M1. Both paratypes are from Thomas Farm.

Referred Specimens.—UF 121133, right m1 or m2; UF 108664, right m3; UF 121135, proximal end of left femur. All referred specimens are from Thomas Farm. MNI is 1. NISP is 6.

Type Locality and Age.—Thomas Farm LF, 12 km NE of Bell, Gilchrist County, Florida, early Miocene, early Hemingfordian (He1).

Occurrence.—*Floridopteryx poyeri* is known only from the Thomas Farm LF.

Etymology.—Named for Arthur Poyer from the FLMNH in recognition of his important contributions to the study of Florida Cenozoic microvertebrates, in particular screenwashing and sorting bats from Thomas Farm.

Diagnosis.—Same as for the genus.

Morphological Descriptons

Upper dentition.—Only one upper tooth of *Floridopteryx poyeri* was identified in the Thomas Farm sample, a shattered but nearly complete right M1 (UF 121134, paratype; Fig. 16), typically the most diagnostic tooth in emballonurids. The tooth is rather heavily worn, especially its lingual half. The posterolabial corner of the tooth is broken off and missing, including the tip of the metacone, metastyle, postmetacrista, part of the premetacrista, and the metacingulum (= postcingulum). As is typical of all other New World emballonurids, the anterolabial portion of the M1 is greatly reduced, in particular the stylar shelf labial to the paracone, preparacrista, and postparacrista (= parafossa or parastylar fovea). However, a fairly well-developed, isolated parastyle is present at the anterolabial termination of the narrow paracingulum (= precingulum). The preparacrista is very short and oriented almost directly labially or slightly anteriorly. The ectoloph on the labial margin of the M1 between the parastyle and mesostyle is gently concave with a slight indentation in the parafossa just anterior to the mesostyle. The mesostyle is a rather prominent bulbous cusp with a distinct anterior orientation. The lingual half of the M1 is squarish in shape, with both the anterior and posterolingual margins of the tooth relatively straight and transverse or horizontal to the anteroposterior axis of the tooth. Because of fairly heavy wear on the lingual portion of the M1, some of the following dental features may have been affected by wear. The narrow paracingulum extends lingually from the parastyle along the anterior margin of the M1, connecting with the preprotocrista and protocone. The protocone is located at the anterolingual corner of

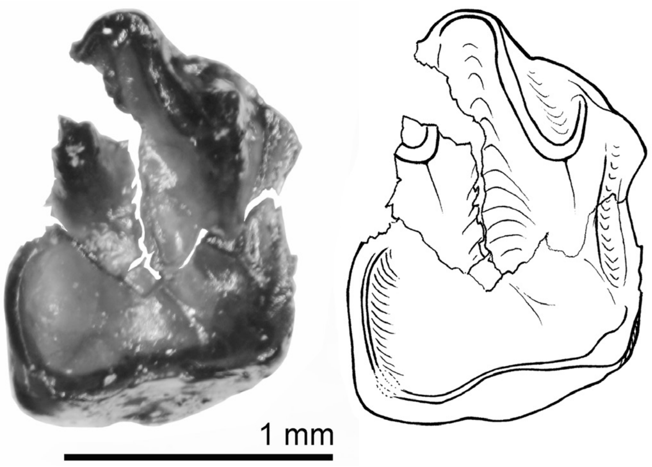

Figure 16. Upper molar of *Floridopteryx poyeri* from Thomas Farm LF. UF 121134, right M1 in occlusal view, photograph and line drawing.

the tooth, slightly anterior to the paracone. The hypocone is barely distinguishable as a low rounded convexity along the posterolingual margin of the tooth. There is no notch in the postprotocrista separating the protocone from the weakly developed hypocone. Deep concavities or pockets are lacking in both the trigon and talon basins. A paraloph and metaloph are present but weak, although they may have been reduced by wear. The talon is squarish in shape, with a straight posterior margin and gently convex lingual margin. The lingual margin of the tooth trends slightly posterolingually from the more labially positioned protocone to the posterolingual corner of the talon.

Lower dentition.—There are three isolated lower molars of *Floridopteryx poyeri* from Thomas Farm, two m1 or m2 (UF 121132, holotype; UF 121133) and an m3 (UF 108664) (Fig. 17; Table 2). We identify the holotype (UF 121132) as an m1 because it was found in close association with a dentary of *F. poyeri* (UF 108661), described below, and the tooth is an exact fit for the m1 alveolus of this dentary. As discussed above under *Oligopteryx*, it is difficult to separate isolated m1s and m2s of emballonurids, so we describe UF 121132 and 121133 together. The m3 is described in the following paragraph. Using the length of the holotype m1, we predict an estimate of the body weight of *F. poyeri* of 12.6 g (by method of Gunnell et al., 2009).

The holotype of *Floridopteryx poyeri* (UF 121132) is virtually unworn, UF 121133 is somewhat more heavily worn. The talonid is much broader than the trigonid, suggesting that both UF 121132 and 121133 are probably m1s. In living New World emballonurids, on m1 the talonid is generally much broader than the trigonid, on m2 it is only slightly broader than the trigonid, and on m3 the trigonid is broader than the talonid. The talonid is also longer than the trigonid because of the anteroposterior compression of the trigonid, reflected in the closely placed paraconid and metaconid along the lingual margin. The metaconid is positioned anterior to the protoconid, such that the protocristid angles anterolingually from the protoconid to the metaconid. The paracristid is gently curved, with a deep V-shaped notch about halfway between the paraconid and protoconid. There is also a deep V-shaped notch in the protocristid halfway between the protoconid and metaconid. The cristid obliqua meets the trigonid directly posterior to the tallest point on the protoconid in UF 121132 but is a bit more lingually placed on UF 121133, meeting the trigonid at the lingual base of the protoconid. In occlusal view, the entocristid is broadly U-shaped on UF 121132 but more sharply V-shaped and penetrates somewhat deeper into the talonid basin on UF 121133. The two m1/m2s of *Floridopteryx* are nyctalodont with the postcristid connecting the hypoconid to the hypoconulid. The hypoconulid is a rather prominent, posteriorly oriented cusp on the extreme posterolingual corner of the tooth immediately behind the entoconid. In lingual view, the paraconid, metaconid, and entoconid are conical with a rounded apex, vertically oriented, and similar in size, with the metaconid and entoconid almost identical in size and the paraconid slightly smaller. In labial view, the protoconid and hypoconid are similar in height, with the protoconid slightly taller; both are easily twice as tall as the three main lingual cusps. The protoconid and hypoconid are also more sharply pointed than the lingual cusps. The anterior cingulum is well-developed, the labial cingulum is not particularly strong,

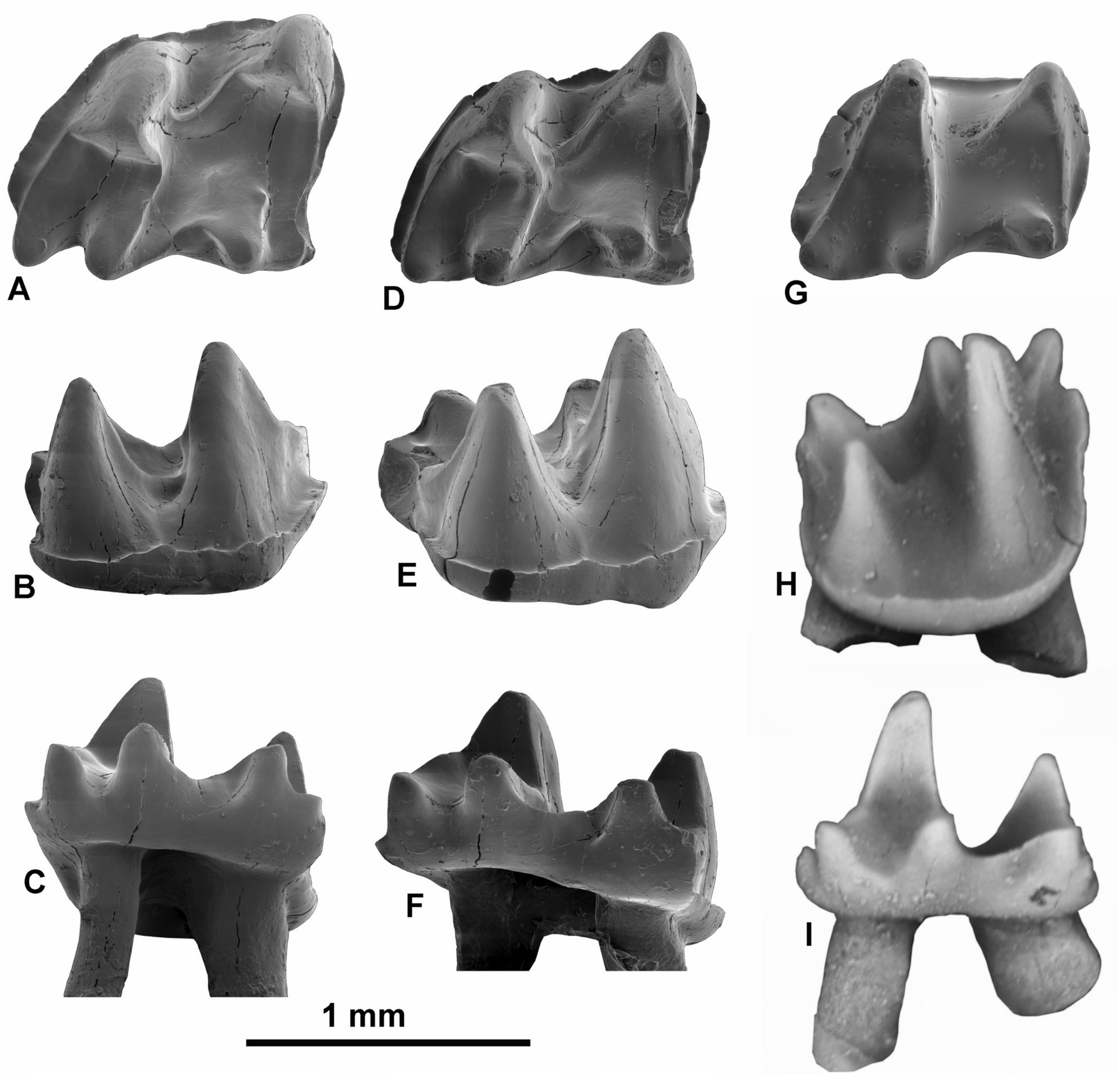

Figure 17. Lower molars of *Floridopteryx poyeri* from Thomas Farm LF. A-C, UF 121132 (holotype), right m1 or m2 in occlusal (and slightly labial, A), labial (B), and lingual (C) views; D-F, UF 121133, right m1 or m2 in occlusal (D), labial (slightly posterior, E), and lingual (slightly posteroventral, F) views; G-I, UF 108664, right m3 in occlusal (G), labial (H), and lingual (I) views.

and the posterior cingulum is weak. The roots on UF 121132 are intact, with the anterior root flattened anteroposteriorly and the posterior root rounded in cross-section. The shape of the roots in this tooth match the shape of the alveoli of m1 in an edentulous mandible (UF 108661) referred to *Floridopteryx poyeri* (see dentary description below), in particular the noticeably flattened anterior root, strongly suggesting that the holotype (UF 121132) is an m1.

A right lower molar (UF 108664) referred to *Floridopteryx poyeri* from Thomas Farm is identified as an m3 based on the broader trigonid compared to the talonid (Fig. 17 G-I). This tooth is identified as an emballonurid by the tall, narrow, V-shaped, labially directed entocristid. The paraconid and metaconid are located close to one another along the lingual margin, although both cusps are more posteriorly positioned than on m1/m2. Because of the more posterior location of the paraconid and metaconid, the paracristid and protocristid meet at a more acute angle than on m1/m2. The paracristid is straight on m3, more curved on m1/m2. The protoconid and metaconid are located at the same level, with the protocristid transverse to the long axis of the tooth. Although the entocristid is sharply V-shaped, it is slightly shallower than on m1/m2. The cristid obliqua meets the trigonid in a more lingual position than on m1/m2, about halfway between the protoconid and metaconid, forming a more acute angle. The hypoconulid is tiny. In lingual view, the entoconid and metaconid are similar in height, vertically oriented, and conical with a rounded apex, the slightly lower paraconid is more anteriorly oriented. In labial view, the protoconid is considerably taller than the hypoconid. The anterior cingulum and labial cingulum are strong; the posterior cingulum is rather weak.

Dentary.—A nearly complete edentulous right dentary (UF 108661, paratype; Fig. 18) from Thomas Farm was collected on the same day and from the same sample of screenwashed concentrate as the holotype of *Floridopteryx poyeri*, an isolated m1 described above (UF 121132). The tooth is an exact fit in the empty alveolus for the m1 in the dentary. It seems unlikely this is a coincidence because emballonurids are otherwise extremely rare from Thomas Farm (six specimens from a sample of more than 3,000 bat fossils). The dentary and tooth are almost certainly from the same individual but became separated during the screenwashing process. However, we have given these specimens separate catalog numbers because we cannot be absolutely certain they belong to the same individual, although without question they belong to the same species, *Floridopteryx poyeri*. We have arbitrarily chosen the m1 (UF 121132) as the holotype and the dentary (UF 108661) as a paratype.

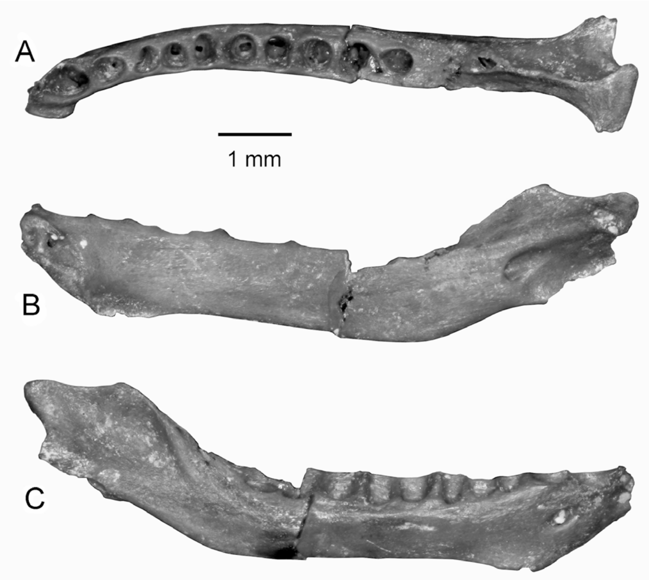

Figure 18. *Floridopteryx poyeri* from Thomas Farm LF. UF 108661, edentulous right dentary, in alveolar (A), lingual (B), and labial (C) views.

The dentary of *Floridopterx* lacks teeth but is otherwise almost perfectly intact, except for missing the tips of the coronoid and angular processes (Fig. 18). It is similar to the dentary of extant emballonurids in having a comparatively elongated mandibular symphysis, reduced coronoid process, and laterally flaring angular process. Dentaries of vespertilionids, the most common Thomas Farm bats in the same size range, generally have a shorter symphysis, tall, rounded coronoid process, and smaller posteriorly oriented angular process. In dorsal aspect, the horizontal ramus of *Floridopterx poyeri* is straight from the m3 anterior to the m1 and then curves gently inward (lingually) toward the symphysis at about the level of p4. The mandibular symphysis is long, extending from the anterior tip of the dentary posteriorly to a point ventral to the anterior alveolus of p4. Ventral to the p2 and p4, a gently rounded ventral projection forms the posteriormost extension of the mandibular symphysis. The symphyseal region and ventral margin of the horizontal ramus anterior to m1 form a gentle obtuse angle. Between p4 and m3 the ventral margin of the horizontal ramus is essentially straight, with only a slight ventral curvature below m3. There are two mental foramina. The posterior mental foramen is large, deep, elliptical in shape, and located ventral to the p2, about one-third the distance between the alveolar and ventral margins of the horizontal ramus. A tiny mental foramen is located much farther anteriorly almost on the mandibular symphysis, immediately ventral to the alveoli for the incisors. The canine alveolus is slightly elliptical in shape, longer in the anteroposterior dimension. The single alveolus of p2 is round and about half the size of the canine alveolus. There is no alveolus for a p3, in agreement with modern New World emballonurids that also lack a p3, but differing from *Oligopteryx* that possesses a tiny, single-rooted p3. The p4 is double-rooted with the posterior alveolus rounded and anterior alveolus somewhat flattened along the anterior margin and set at a slight angle to the toothrow. There is no diastema between c1 and p2 and a very short diastema between p2 and p4. Five of the six molar alveoli are rounded in shape, but the anterior alveolus of the m1 is distinctly flattened anteroposteriorly. An examination of the well-preserved and complete roots of the m1 of *Floridopteryx poyeri* that we believe is associated with this dentary (UF 121132, holotype), confirms that the anterior root is flattened anteroposteriorly while the posterior root is round in cross-section.

As is typical of emballonurids, the ascending ramus of the dentary is upturned dorsally posterior to the toothrow in *Floridopteryx*, although not to the degree observed in certain other members of this family such as *Peropteryx* and *Saccopteryx*. The tip of the coronoid process is missing but the base indicates that it was clearly rather short and slender dorsally as in emballonurids, and unlike the taller, broader, more rounded coronoid of most vespertilionids. The angular process is located at about the same level as the alveolar margin of the mandibular toothrow and, although its tip is broken, it has a distinct lateral orientation. In dorsal view, the angular process flares noticeably lateral to the lateral edge of the horizontal ramus. The articular process or condyle is intact and is located dorsal to the alveolar margin of the toothrow. In posterior view, the articular process has a flat to slightly concave dorsal articular surface, a convex ventral margin, and is comparatively deep in the dorsoventral dimension. The mandibular foramen on the lingual surface of the dentary is large, deep, elliptical in shape, oriented anteroposteriorly, and is located just ventral to the toothrow below the tip of the coronoid. In *Peropteryx* and *Saccopteryx*, the mandibular foramen is much smaller, more rounded, and is located dorsal to the alveolar margin of the toothrow, reflecting the more strongly dorsally upturned ascending ramus in these two genera.

Femur.—A single proximal end of a left femur (UF 121135) referred to *Floridopteryx poyeri* is the only emballonurid postcranial element identified in the Thomas Farm sample (Fig. 19). This specimen is similar to, although somewhat smaller than, a proximal femur of *Oligopteryx floridanus* from Brooksville 2 described above. The femoral head is generally spheroidal but is slightly flattened proximally with a well-developed, rounded fovea capitis. The head is located in the center of the shaft but is slightly canted or angled medially and has a distinct neck separating it from the shaft. The lesser trochanter is slightly larger and extends farther proximally than the greater trochanter. The lesser trochanter is elongated with a rather pointed tip, while the greater trochanter is shorter with a blunt squarish tip. There is a well-developed medial ridge on the medial edge of the shaft distal to the lesser trochanter.

COMPARISONS WITH OTHER GENERA OF EMBALLONURIDAE

We compared *Floridopteryx poyeri* from Thomas Farm to all 14 living genera and the seven other extinct genera of Emballonuridae, *Tachypteron*, *Vespertiliavus*, *Pseudovespertiliavus*, *Dhofarella*, and *Afrillonura* from the Old World, and *Oligopteryx* and *Karstopteryx* from the Oligocene of Florida (see list of modern comparative material examined in Appendix 1). Dental characters of selected extinct and living species of Emballonuridae are presented in Table 4 and Appendix 2. Among other extinct genera of emballonurids, we consider the comparisons of *Floridopteryx* with *Oligopteryx* and *Karstopteryx* to be the most critical based on their close geographic occurrence and possible

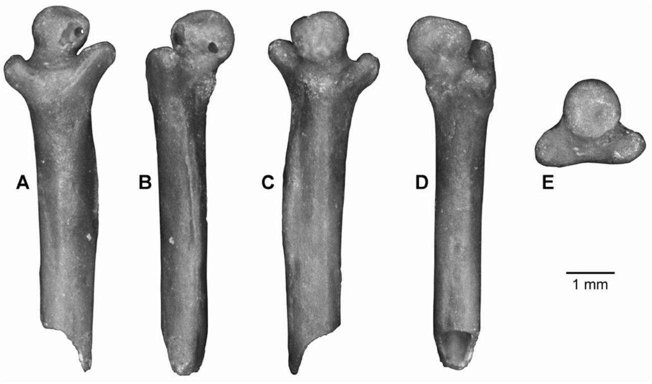

Figure 19. *Floridopteryx poyeri* from Thomas Farm LF. UF 121135, left proximal femur, in ventral (A), anterior (B), dorsal (C), posterior (D), and proximal end (E) views.

phylogenetic relationship. These are the only three described extinct genera of emballonurids from the New World.

Features that distinguish the M1 of *Floridopteryx* from the two species of *Oligopteryx*, *O. floridanus* and *O. hamaxitos*, are the well-developed parastyle, weak paracingulum, bulbous anteriorly directed mesostyle, weak hypocone, shallow concavities in the trigon and talon basins (may be partially obscured by heavy wear), and the truncated and squarish talon, especially the posterior margin. *Floridopteryx* shares several of these features, including a well-developed parastyle and reduced hypocone not separated from the protocone by a notch in the postprotocrista, with *Karstopteryx gunnelli* from the latest Oligocene Buda LF. Compared to *F. poyeri*, the M1 of *K. gunnelli* is much larger and has a more prominent parastyle with a rounded anterior projection. The characters of the M1 shared by *F. poyeri* and *K. gunnelli* but not the two species of *Oligopteryx*, suggest the possibility that *Floridopteryx* may have evolved from a species similar to *K. gunnelli* in the early Miocene (latest Arikareean or earliest Hemingfordian).

The lower molars of *Floridopteryx* and those of *Oligopteryx floridanus* and *O hamaxitos* are similar, but there are differences. Both genera have the talonid broader than the trigonid on m1 and m2, but the talonid is relatively broader in *Floridopteryx*. The trigonid is compressed anteroposteriorly with the paraconid and metaconid close together along the lingual margin in both genera, but the metaconid is more anterior in *Floridopteryx*. Because of the more anterior location of the metaconid in *Floridopteryx*, the protocristid is even more strongly angled anterolingually from the protoconid to the metaconid. The entoconid is located more anteriorly, the hypoconulid is smaller, and the entocristid is more labially inflected in *Floridopteryx*. On the m3, the metaconid is located farther posteriorly in *Floridopteryx* and the protocristid is at a right angle to the long axis of the tooth, not slightly angled as in the m3 of *Oligopteryx*. There are also differences between these two genera in the structure of the dentary, the most important of which is the lack of a p3 alveolus in *Floridopteryx* and the presence of this alveolus (and tooth) in *Oligopteryx*. No lower teeth are known of *Karstopteryx* excluding comparisons with the lower dentition of *Floridopteryx*.

Floridopteryx is readily distinguished from the two European Eocene emballonurid genera *Tachypteron* and *Vespertiliavus*. Both of these genera possess a p3, which is lacking in *Floridopteryx*. Compared to *Tachypteron* and *Vespertiliavus*, the parastylar region of M1 is strongly reduced in *Floridopteryx* with a small parastyle and shorter preparacrista. In addition, the M1 of *Floridopteryx* differs from *Vespertiliavus* in the near absence of a hypocone and the smaller talon with a straight (not posteriorly expanded) posterior margin. The lower molars are difficult to compare in the two specimens of *Tachypteron franzeni* from the middle Eocene Messel site in Germany, both of which have the upper and lower dentitions tightly occluded (Storch et al., 2002). Differences that can be observed include the weaker labial cingula on the lower molars and the more reduced coronoid process of the dentary in *Floridopteryx*. Compared to two species of *Vespertiliavus* recently described from the early to middle Eocene of Tunisia in northern Africa (Ravel et al., 2016), the m1 and m2 of *Floridopteryx* have a much broader talonid compared to the trigonid, a taller and more vertical paraconid, more closely placed paraconid and metaconid, more posteriorly directed protocristid owing to the more anterior location of the metaconid, larger entoconid, and more labially inflected entocristid. The genus *Pseudovespertiliavus*, recently described from the early to middle Eocene of Algeria in northern Africa (Ravel et al., 2016), is similar to *Vespertiliavus* and differs from *Floridopteryx* in the same characters that the Florida Miocene genus differs from *Vespertiliavus*.

There are two described species of the extinct emballonurid genus *Dhofarella*, one from the late Eocene of Egypt and the second from the early Oligocene of Oman (Sigé et al., 1994; Gunnell et al, 2008). Only *D. thaleri* from Oman has the M1 preserved. Compared to *D. thaleri*, the M1 of *Floridopteryx* has a smaller parastyle and reduced parastylar region, shorter labially oriented preparacrista, shallower notch in the parafossa labial to the paracone, and a straight (rather than rounded) posterior margin of the talon basin. Neither species of *Dhofarella* preserves the dentary anterior to the m1, so the presence or absence of p3 in this genus cannot be determined. The m1 and m2 of *Floridopteryx* differ from those of *Dhofarella* in the broader talonid, more closely placed paraconid and metaconid, taller and more vertical paraconid, strongly angled protocristid from the more anteriorly placed metaconid to the protoconid, and the sharp labial inflection of the entocristid.

Compared with the recently described middle Miocene emballonurine *Afrillonura namibensis* ffrom the Berg Aukas 1 site in the Otavi Mountain karst deposits of Namibia (Rosina and Pickford, 2021), the M1 of *Floridopteryx* differs in having a smaller parastyle, longer preparacrista, weaker paraloph and metaloph, poorly developed hypocone, and lack of a notch in the postprotocrista separating the protocone and hypocone. Compared to the m1 of *Afrillonura*, the m1 of *Floridopteyx* has the trigonid more compressed and shorter anteroposteriorly with the paraconid and metaconid closer together, and the postcristid more strongly angled posterolabially from the more anteriorly located metaconid to the protoconid.

The two genera in the Old World emballonurid subfamily Taphozoinae, *Taphozous* and *Saccolaimus*, are very similar dentally, and have in the past been considered congeneric. Our comparisons of *Floridopteryx* apply to both *Taphozous* and *Saccolaimus*. The M1 of *Floridopteryx* differs from the M1 of the two taphozoines in its smaller size, overall shape of the tooth (more anteroposteriorly compressed in *Floridopteryx*, squarish in taphozoines), reduced parastylar area, much smaller parastyle, presence of a paracingulum, more closely placed paracone and metacone, and a squarish talon basin. Compared to taphozoines, the lower m1 and m2 of *Floridopteryx* have an anteroposteriorly compressed trigonid, much broader talonid, more posterior position of the paraconid located close to the metaconid, anterolingually angled protocristid from the more posterior protoconid to the more anteriorly placed metaconid and V-shaped entocristid oriented labially.

Floridopteryx differs in several dental features from the Old World emballonurine genera *Emballonura*, *Mosia*, and *Paremballonura*, all of which were at one time included in *Emballonura*. The M1 of *Floridopteryx* is narrower anteroposteriorly and wider in the transverse or labiolingual dimension (squarish in *Emballonura* except for talon), the ectoloph is not as shallow, the paracone and metacone are located farther apart and both in a more lingual position, the trigon and talon basins are not deeply pocketed, and the hypocone is very weak and is not separated from the protocone by a prominent notch in the postprotocrista. In several characters, the lower molars of *Emballonura*, *Mosia*, and *Paremballonura* are similar to taphozoines and differ from *Floridopteryx.* Compared to these three genera, the lower m1 and m2 of *Floridopteryx* have a compressed trigonid with the paraconid and metaconid close to one another, the metaconid is anterior to the protoconid the talonid is broader, the talonid basin lacks a deep concave pit, the cristid obliqua meets the trigonid at a more acute angle, the entocristid is strongly curved/angled and is oriented labially, and the hypoconulid is more prominent.

Dentally, the living African emballonurine genus *Coleura* is more similar to *Floridopteryx* and several genera of New World emballonurines than are *Emballonura*, *Mosia*, and *Paremballonura*. The M1 of *Floridopteryx* is similar in size to that of *Coleura* but the parastyle is better developed and extends well anterior to the paracingulum, a short preparacrista is present, a paraloph is absent and the metaloph is weak, a deep concavity is lacking in the trigon basin, and the hypocone is highly reduced. Compared to *Coleura*, the m1 and m2 of *Floridopteryx* have the trigonid more compressed, the metaconid is more anterior, the protocristid is oriented anterolingually from the protoconid to the metaconid, the cristid obliqua meets the trigonid at a more acute angle and connects to the trigonid in a more lingual position, and the entocristid is more labially inflected.

Our comparisons indicate that the Florida early Miocene genus *Floridopteryx* is the oldest member of the endemic New World emballonurid tribe Diclidurini (See discussion above of the systematic relationships of *Oligopteryx* regarding the possibility this genus may also be an early diclidurine). We compared fossils of *Floridopteryx* to at least one species in each of the eight extant genera of New World diclidurines, that have been further subdivided into two subtribes (Lim, 2007; Lim et al., 2008): the Diclidurina (*Balantiopteryx*, *Cormura*, *Cyttarops*, *Diclidurus*, and *Peropteryx*) and the Saccopterygina (*Centronycteris*, *Rhynchonycteris*, and *Saccopteryx*). The comparisons are in alphabetical order within each of the two diclidurine subtribes, beginning with the Diclidurina.

Compared to *Balantiopteryx*, the M1 of *Floridopteryx* is larger and also differs in other features including the overall shape of the tooth, which is broader in the transverse dimension causing the paracone and protocone to be more widely separated, more lingual location of the parastyle, longer preparacrista, better developed mesostyle, shallower concavity in the trigon basin, and very weak hypocone. The m1/m2 of *Floridopteryx* and *Balantiopteryx* are similar in the strong anteroposterior compression of both the trigonid and talonid and by the much broader talonids compared to the trigonids, but the lower molars of *Floridopteryx* differ in the separation of the paraconid and metaconid by a deeper notch, larger and more bulbous entoconid located in a more anterior position closer to the metaconid, and the location of the hypoconulid directly posterior to the entoconid.

The M1 of *Floridopteryx* and *Cormura* are more similar than the Florida fossil is to most other extant genera of emballonurids, but there are some differences. The M1 of *Floridopteryx* is somewhat broader transversely, the parastyle is smaller and located more lingually, the protocone is in a more lingual position and more widely separated from the paracone, and the mesostyle is larger and more bulbous. Compared to *Cormura*, the m1 of *Floridopteryx* has the trigonid more compressed with the paraconid located more posteriorly and the metaconid more anteriorly, the paraconid is taller and on the lingual margin, the protocristid angles anterolingually from the protoconid to the metaconid, and the cristid obliqua forms a more acute angle where it meets the trigonid. The talonid of m3 is broader in *Floridopteryx*.

The M1 of *Floridopteryx* differs from that of the diclidurine *Cyttarops* in the lower, more rounded cristae, larger parastyle, more prominent preparacrista, narrow paracingulum, more posterior position of the protocone, the near absence of a hypocone, and the less prominent concavities in the trigon and talon basins. The m1/m2 of *Floridopteryx* differ from the lower molars of *Cyttarops* in the lower and more bulbous cusps, more posterior location and vertical orientation of the paraconid, closely placed paraconid and metaconid, anterolingual orientation of protocristid from protoconid to metaconid, much broader talonid, and larger hypoconulid.

The M1 of *Floridopteryx* differs from *Diclidurus* in the presence of a larger parastyle located somewhat lingual to the anterolabial margin, broader paracingulum, more lingual position of the paracone, better developed mesostyle located more anteriorly, lack of deep concavities in the trigon and talon basins, and the near absence of a hypocone. The m1/m2 of *Floridopteryx* differs from *Diclidurus* in the much broader talonid compared to trigonid, strong anteroposterior compression of both the trigonid and talonid, closely placed paraconid and metaconid, larger paraconid located more posteriorly, more anterior location of the metaconid, entocristid more sharply angled labially, and a larger hypoconulid.

Compared to *Peropteryx*, the M1 of *Floridopteryx* is broader transversely with the protocone positioned more lingually, lacks a deep concave pit in the trigon basin, and the hypocone is very weak. The m1/m2 of *Floridopteryx* differ from these lower molars of *Peropteryx* in having a broader talonid compared to the trigonid, paraconid vertical, metaconid more anterior and closer to the paraconid, protocristid strongly angled, cristid obliqua forming a more acute angle and meeting the trigonid farther lingually, and entocristid not as sharply V-shaped and less labially inflected.

The M1 of *Floridopteryx* differs from *Centronycteris* in its much larger size, lack of a deep V-shaped notch in the parafossa labial to the paracone, more lingual location of the paracone and protocone, lack of deep pits in the trigon and talon basins, and the near absence of a hypocone. The m1/m2 of *Floridopteryx* and *Centronycteris* are similar in size but *Floridopteryx* has the paraconid located more posteriorly, the protocristid angled anteriorly from the protoconid to the metaconid, the cristid obliqua forming a more acute angle connecting to the trigonid about halfway between the protoconid and metaconid, lacking a deep pit in the talonid basin, less sharply V-shaped entocristid that does not extend as far labially, and larger hypoconulid.

Rhynchonycteris is the smallest New World emballonurid and differs from *Floridopteryx* in many dental features besides its much smaller size. Compared to *Rhynchonycteris*, the M1 of_*Floridopteryx* has all cristae on the ectoloph somewhat lower and thicker and not sharp and blade-like, weaker parastyle, paracone and metacone located farther from the labial margin, lack of deep concave pits in the trigon and talon basins, and a very weak hypocone. The m1/m2 of *Floridopteryx* are shorter in the anteroposterior dimension, the protoconid is in a more posterior position, the paraconid and metaconid are not as close together, the metaconid is smaller, the lingual margin of the talonid is not as deeply concave because the entocristid is not a sharply deflected labially, and the entoconid is not laterally compressed.

Among extant New World diclidurines, *Floridopteryx poyeri* is most similar in size and dental morphology to *Saccopteryx*, specifically the species *S. bilineata*. However, there are notable differences between *Floridopteryx* and *Saccopteryx*. Compared to *Saccopteryx*, the M1 of *Floridopteryx* has a somewhat smaller parastyle that does not extend as far anteriorly, the protocone is more lingual and farther from the paracone, and the trigon basin lacks a deep elliptically shaped pit or concavity. In the lower molars (m1/m2) of *Floridopteryx*, the talonid is relatively broader, the talonid basin lacks a deep pit, the paraconid is more vertical, the metaconid is more anterior, the paraconid and metaconid are closer to one another, the protocristid is oriented at an angle to the long axis of the tooth, the cristid obliqua forms a more acute angle and attaches to the trigonid farther lingually, the entoconid is larger and more inflated, the entocristid not as sharply V-shaped and is less labially inflected, and the hypoconulid is larger.

The proximal end of the femur of *Floridopteryx* differs from the femur of both *Oligopteryx* and the extant emballonurid *Saccopteryx*. The greater and lesser trochanters of *Floridopteryx* and *Saccopteryx* are similar in size and morphology, with the lesser trochanter more elongated and extending farther proximally than the greater trochanter. In *Oligopteryx*, the two trochanters extend proximally to the same level and the lesser trochanter is shorter, more robust, and triangular in shape. The femoral head is comparatively larger in *Oligopteryx*, approximately equal in width to the width of the shaft. The head is narrower than the shaft in *Floridopteryx*. The femoral head of *Saccopteryx* is larger and is not canted medially compared to *Floridopteryx*.

DISCUSSION

SYSTEMATIC RELATIONSHIPS

Previous analyses of the systematic relationships within the family Emballonuridae include Barghoorn (1977) based on cranial and dental characters, Robbins and Sarich (1988) from protein electrophoresis and immunology, Griffiths and Smith (1991) on hyoid morphology, and more recent studies on molecular genetics (Lim, 2007; Lim et al., 2008; Goodman et al., 2012; Ruedi et al., 2012; Uvizl et al., 2019). Studies of both morphological and molecular characters demonstrate two major dichotomies among living species in the Emballonuridae. The first separation is between the strictly Old World subfamily Taphozoinae, including the genera *Taphozous* and *Saccolaimus*, and the subfamily Emballonurinae, including four genera from the Old World and eight Neotropical genera. The second major dichotomy occurs within the Emballonurinae, between the Old World tribe Emballonurini (*Emballonura*, *Coleura*, *Mosia,* and *Paremballonura*) and the New World tribe Diclidurini. Finally, the Diclidurini have been separated into two subtribes (Lim, 2007; Lim et al., 2008), the Diclidurina (*Balantiopteryx*, *Cormura*, *Cyttarops*, *Diclidurus*, and *Peropteryx*) and the Saccopterygina (*Centronycteris*, *Rhynchonycteris*, and *Saccopteryx*). The diclidurines are a monophyletic group that had a common origin, presumably from either Africa or North America via Eurasia as discussed below.

Not surprisingly, the earliest fossil representatives of the Emballonuridae are also the most primitive. Four extinct genera of emballonurids have been described from Eocene and Oligocene faunas in the Old World: *Vespertiliavus* from the early to middle Eocene of Tunisia (Ravel et al., 2016) and the middle Eocene to Oligocene of Europe (Barghoorn, 1977; Sigé, 1990; Smith et al., 2012; Maitre, 2014); *Pseudovespertiliavus* from the early to middle Eocene of Algeria (Ravel et al., 2016); *Tachypteron* from the middle Eocene of Germany (Storch et al., 2002; Smith et al., 2012); and *Dhofarella* from the late Eocene of Egypt (Gunnell et al., 2008) and the early Oligocene of Oman on the Arabian peninsula (Sigé et al., 1994). It is difficult to evaluate certain characters in two of these genera, *Dhofarella* and *Pseudovespertiliavus*, represented almost entirely by isolated teeth, for example, the presence or absence of p3. Both *Tachypteron* and *Vespertiliavus* have a well-developed, double-rooted p3, the primitive condition for the Emballonuridae. The only other emballonurid known to possess a p3 is the Oligocene *Oligopteryx* from Florida, in which this tooth is very small and single-rooted. All living members of the Emballonuridae, including both Taphozoinae and Emballonurinae, as well as the early Miocene *Floridopteryx* from Florida, lack a p3. All four Eocene/Oligocene genera of Old World emballonurids are represented by the M1, the most diagnostic tooth in the Emballonuridae. Three of these genera, *Tachypteron*, *Vespertiliavus*, and *Pseudovespertiliavus*, have a well-developed parastylar region on the anterolabial margin of the M1, including a prominent parastyle, long preparacrista, strong paracingulum (= precingulum), and wide shelf labial to the paracone (= parafossa of Ravel et al., 2016). Compared to these three Eocene genera, as well as the living taphozoines *Taphozous* and *Saccolaimus*, *Dhofarella thaleri* from the early Oligocene of Oman (Sigé et al., 1994) has the parstylar area on the M1 more reduced, with a shorter preparacrista and reduced shelf labial to the paracone. However, when compared to most living emballonurines, as well as *Oligopteryx*, *Karstopteryx*, and *Floridopteryx* from Florida, the parastylar region in *Dhofarella* is better developed, with a longer preparacrista, wider shelf labial to the paracone (parafossa) with a noticeable V-shaped notch, larger parastyle, and broader paracingulum. Rosina and Pickford (2021) considered *Dhofarella* to be the oldest member of the Emballonurinae. They also regarded their recently described extinct genus *Afrillonura* from the middle Miocene of Namibia in southwestern Africa to be an emballonurine, similar in dental characters to the extant African emballonurine genus *Coleura* (Rosina and Pickford, 2021).

Ravel et al. (2016) presented a phylogenetic analysis of 65 dental and mandibular characters of four extinct Old World genera of Emballonuridae, including one species each of *Dhofarella*, *Pseudovespertiliavus*, and *Tachypteron*, and five species of *Vespertiliavus*, as well as two living species of Old World emballonurids, *Emballonura* (= *Paremballonura*) *atrata* and *Taphozous melanopogon*. No New World emballonurids (Diclidurini) were included in their analysis. Their phylogeny placed the three oldest genera at the base of the tree, all known from either the early or middle Eocene, with *Tachypteron* in the basalmost position, followed next by *Pseudovespertiliavus*, and then the five species of *Vespertiliavus*. Ravel et al. (2016) placed their new genus and species, *Chambinycteris pusilli*, from the early to middle Eocene Chambi fauna in Tunisia, at the very base of the emballonurid clade, although they considered *Chambinycteris* to be "family indeterminate" in their taxonomic analysis. In the Ravel et al. (2016) phylogeny, the extinct genus *Dhofarella* from the late Eocene and early Oligocene was placed closer to the modern genera *Taphozous* and *Emballonura* (= *Paremballonura*) than to *Tachypteron*, *Pseudovespertiliavus*, and *Vespertiliavus*. It is difficult to assess the relationship of *Dhofarella* to living emballonurids based on the Ravel et al. (2016) phylogeny because they included only two modern taxa, one taphozoine and one Old World emballonurine. Gunnell et al. (2008) noted that *Dhofarella sigei* from the late Eocene of Egypt was most similar to the African emballonurine genus *Coleura* among living emballonurids. As mentioned above, Rosina and Pickford (2021) also considered the extinct middle Miocene genus *Afrillonura* to be closely related to *Coleura* and placed both *Afrillonura* and *Dhofarella* in the Emballonurinae.

Considering that all currently known Eocene emballonurids are from either Europe or northern Africa, it seems likely that the Emballonuridae had an Old World origin. New World emballonurids were derived from Old World emballonurids sometime prior to the oldest Western Hemisphere occurrence of this family in the early Oligocene (~30 Ma) of Florida. With the possible exception of the incompletely known late Eocene and early Oligocene *Dhofarella*, the Oligocene fossils of *Oligopteryx floridanus* and *O. hamaxitos* from I-75 and Brooksville 2 in Florida are among the oldest records of the Emballonurinae and may also be the earliest members of the Diclidurini. However, based on the presence of a p3, *Oligopteryx* appears to be more primitive than the remainder of the New World emballonurid assemblage. The latest Oligocene *Karstopteryx* is closely related to *Oligopteryx* and may also be an early diclidurine. We hesitate to name a new, higher-level taxon based on fragmentary fossil material, but the Florida Oligocene emballonurids may represent an extinct subtribe of the Diclidurini. The Thomas Farm LF contains a third extinct genus of New World Emballonuridae, *Floridopteryx*. In contrast to *Oligopteryx*, *Floridopteryx* lacks the p3, and the M1 has several features that are more similar to the living or crown group of Neotropical emballonurids (Diclidurini). Owing to the incomplete and fragmentary condition of the fossil sample of *Floridopteryx*, we are not able to determine to which of the two diclidurine subtribes (Diclidurina or Saccopterygina) this extinct genus belongs.

We did not conduct a phylogenetic analysis of *Oligopteryx*, *Karstopteryx*, and *Floridopteryx*, New World diclidurines, and living and extinct Old World emballonurids, although we did make morphological comparisons of the extinct Florida genera to all living and extinct genera of emballonurids (See Comparisons sections in the taxonomic accounts of *Oligopteryx floridanus* and *Floridopteryx poyeri*). A phylogenetic analysis in Ravel et al. (2016) included most extinct species of emballonurids, with the exception of the recently described *Afrillonura namibensis* (Rosina and Pickford, 2021), together with several archaic genera of Eocene bats belonging to extinct families (e.g., *Icaronycteris*, *Archaeonycteris*, *Palaeochiropteryx*), several enigmatic Eocene genera (*Chambinycteris*, *Chibanycteris*, *Khoufechia*), as well two living Old World species of emballonurids (*Taphozous melanopogon* and *Emballonura* = *Paremballonura atrata*) and two living species in the Nycteridae (*Nycteris gambiensis*, *N. grandis*). Their phylogenetic analysis was based on dental and mandibular characters in the groups listed above.

We produced a table (Table 4) that assesses dental and mandibular characters in all eight extinct genera of emballonurids, including the five extinct genera from the Old World (*Afrillonura*, *Dhofarella*, *Pseudovespertiliavus*, *Tachypteron*, and *Vespertiliavus*) and the three new extinct genera from the Oligocene and Miocene of Florida described herein (*Floridopteryx*, *Karstopteryx*, and *Oligopteryx*), as well as species representing six living genera of emballonurids, including a taphozoine (*Taphozous*), an emballonurine (*Coleura*), and four diclidurines (*Balantiopteryx*, *Diclidurus*, *Peropteryx*, and *Saccopteryx*). Characters 1–65 in Table 4 were originally proposed by Ravel et al. (2016) in their phylogenetic analysis of the Emballonuridae, as well as several outgroups mentioned above. In our evaluation of characters from Ravel et al. (2016) that are present in the Florida fossil emballonurids, we noticed that many of these characters are useful in separating fossil and modern emballonurids from archaic Eocene bats and nycterids but are not as helpful in elucidating relationships within the Emballonuridae. Therefore, we added 20 dental characters to Table 4 (Characters numbered 66–85, under New Characters–this study) that our comparisons indicated were more informative in separating genera within the Emballonuridae and are particularly important in evaluating the relationships of the Florida fossils. Our Table 4 is limited to Emballonuridae and includes 14 species, nine of which were not analyzed by Ravel et al. (2016): the newly described Miocene species from Namibia *Afrillonura namibensis*; the extant African emballonurine species *Coleura afra*; three extinct species of Florida emballonurids, *Oligopteryx floridanus*, *Karstopteryx gunnelli*, and *Floridopteryx poyeri*; and four living species of New World diclidurine emballonurids, *Balantiopteryx plicata*, *Diclidurus albus*, *Peropteryx macrotis*, and *Saccopteryx bilineata*. Because the six extant emballonurid genera in Table 4 are each represented by more than one species, we examined at least two species within a genus to make certain the species we analyzed were representative of the genera. Appendix 2 provides a list of the 85 dental and mandibular characters evaluated in Table 4, providing detailed descriptions of both the charcters and character states within each character.

We feel that the limited number of characters available in the Florida Oligocene and Miocene emballonurid fossils would be insufficient to generate a robust phylogenetic analysis of the New World Emballonurinae (Diclidurini) or of the Emballonuridae in general. Recent work has emphasized the desirability of using an approach toward deriving phylogenetic hypotheses using multiple integrated lines of evidence and congruent datasets (Solari et al. 2019) that are not yet available in the fossil emballonurids and their extant relatives. Therefore, we elect to provide a suite of potentially phylogenetically informative dental and mandibular characters that are available in the Florida emballonurid fossils (Table 4, Appendix 2) that could be added to larger databases of morphological characters for extant taxa (for example, from various systems of the soft anatomy). These characters could be incorporated with genomic and other types of data to perform even more comprehensive and robust phylogenetic analyses.

Taphonomy and Paleoecology

All fossil specimens of Florida Oligocene and early Miocene Emballonuridae are derived from paleokarst deposits. Emballonurids are unknown in Florida mid Tertiary bat sites from non-karst depositional environments, including the late Oligocene White Springs LF and several early Miocene sites (Morgan and Czaplewski, 2012). The two most productive fossil sites for emballonurids in Florida, the early Oligocene I-75 LF and late Oligocene Brooksville 2 LF, consist of terrestrially derived clay and sand deposits filling small pockets or fissures in Paleogene marine limestones that represent remnants of former caves (Patton, 1969a; Hayes, 2000; Morgan and Hulbert, 2008). The taphonomy of these two sites is consistent with cave deposits, containing substantial samples of small mammals, including abundant bats, as well as other small vertebrates (mostly amphibians and reptiles, birds are rare or absent), and isolated teeth and small postcranial elements of larger mammals (Hayes, 2000; Holman and Harrison, 2001; Morgan and Hulbert, 2008). The large emballonurid *Oligopteryx floridanus* is the most common bat in the Brooksville 2 fauna, with a sample consisting of an NISP (number of identifiable specimens) of more than 100, representing seven individuals, comprising about half of the chiropteran fossils from this site. The second most abundant bat in the Brooksville 2 LF is the mormoopid *Koopmanycteris palaeomormoops*, represented by about 50 specimens (Morgan et al., 2019). These same two species, the emballonurid *O. floridanus* and the mormoopid *K. palaeomormoops*, are also the most common bats in the I-75 fauna. A smaller emballonurid, *O. hamaxitos*, is also present in Brooksville 2 and I-75 but is rather uncommon with two individuals in each fauna. The samples of mormoopid fossils in the I-75 and Brooksville 2 karst deposits are consistent with our proposed taphonomic scenario for these two sites, since almost all species in the Mormoopidae roost in caves (Smith, 1972). A partial radius representing an indeterminate genus in the Natalidae is also known from I-75, and all living natalids are obligate cavernicoles (Morgan and Czaplewski, 2003; Tejedor, 2011). The abundance of *Oligopteryx* in the two Florida Oligocene karst sites suggests these emballonurids were also cave dwellers.

In the context of elucidating the evolutionary history of roosting ecology in the Emballonuridae, it is instructive to examine the roosting habits of living members of this family. Most extant New World species of emballonurids roost in trees, including recesses between buttresses on the outside of trees, underneath fallen trees, within hollow trees, and under leaves (Nowak, 1994; Simmons and Voss, 1998). Several species of Neotropical emballonurids are known to roost in caves, including *Balantiopteryx io*, *B. plicata*, *Peropteryx macrotis*, and *Saccopteryx bilineata* (Goodwin and Greenhall, 1961; Nowak, 1994; Simmons and Voss, 1998; Ceballos et al., 2014). Goodwin and Greenhall (1961, p. 216) noted tbat *Peropteryx macrotis* "…has been found on Tobago roosting in association with *Glossophaga longirostris* in well-lighted limestone and coral caves that overlook the ocean." Old World species of emballonurids more commonly roost in caves than do New World members of this family (Hill and Smith, 1984; Nowak, 1994). Species in the taphozoine genus *Taphozous* are called tomb bats for their tendency to roost in tombs, caves, or rock crevices, and species in the emballonurine genera *Emballonura* and *Coleura* also often roost in caves (Nowak, 1994; Bambini et al. 2006; Nkrumah et al., 2021).

Among extinct Old World genera of Emballonuridae, most species in the genus *Vespertiliavus* from the Eocene and Oligocene in France and elsewhere in western Europe are from karst deposits that probably represent former caves (Sigé and Legendre, 1983; Maitre, 2014). Fossils of the recently described extinct emballonurine genus *Afrillonura* and associated taphozoines in the genera *Taphozous* and *Saccolaimus,* from Namibia in southwestern Africa, are from Miocene cave-derived karst deposits (Rosina and Pickford, 2020, 2021). King et al. (2020) reported *Taphozous* and *Saccolaimus* from an early Pleistocene site in the Riversleigh World Heritage Area in Australia, consisting of an extensive series of karst deposits.

The evidence from the Brooksville 2 and I-75 sites, including the geology, taphonomy, and vertebrate fauna, in particular the abundance of bats, strongly indicates that both species of *Oligopteryx* were cavernicolous. This suggests a different paleoecology for the Florida Oligocene emballonurids compared to the majority of modern Neotropical species in this family, as noted above. The early Oligocene I-75 LF and late Oligocene Brooksville 2 LF are the oldest karst deposits in North America known to contain bats (Czaplewski et al., 2008; Morgan and Czaplewski, 2012; this paper). Consequently, the two species of emballonurids (*Oligopteryx floridanus* and *O. hamaxitos*) and one species of mormoopid (*Koopmanycteris palaeomormoops*) described from these two sites, as well as a natalid from I-75 (Morgan and Czaplewski, 2003), are the oldest known cave-dwelling bats in the Western Hemisphere, taking into consideration the lack of pre-Pleistocene karst deposits in South America containing fossil bats.

The early Miocene Thomas Farm site is also a paleokarst deposit, but the taphonomy and vertebrate fauna are quite different from the Brooksville 2 and I-75 sites. Thomas Farm is a large, deep (>30 m), sediment-filled sinkhole that accumulated significant samples of both large mammals and small vertebrates, including abundant bats (Pratt, 1989, 1990). The proposed taphonomic setting for the large sample of bats in the Thomas Farm LF is the presence of vertical limestone walls in the sinkhole containing a cave or caves that supported colonies of cave-dwelling bats (Pratt, 1989). Although bat fossils occur throughout the stratigraphic section in the Thomas Farm site, they are concentrated in certain layers, in particular a lime sand near the top of the section. This lime sand contains large samples of bats and other small vertebrates (rodents, amphibians, lizards, snakes, and birds) but a rather limited sample of larger mammals, suggesting this layer may represent a former cave deposit. The majority of bat fossils from Thomas Farm (>75%, consisting of several thousand specimens) belong to *Suaptenos whitei*, an extinct genus and species in the family Vespertilionidae that was almost certainly a colonial cavernicolous bat. The second most common bat at Thomas Farm, *Primonatalus prattae*, is one of the earliest known members of the Natalidae, a family composed entirely of cave-dwelling species (Morgan and Czaplewski, 2003, 2012; Tejedor, 2011). Emballonuridae are rare at Thomas Farm, with only six specimens of *Floridopteryx poyeri* from a sample of more than 3,000 bat fossils (<1% of the total chiropteran fauna from this site). The rarity of *Floridopteryx* at Thomas Farm suggests this bat may not have been a cave dweller. This would support our hypothesis that *Floridopteryx* is a member of the Diclidurini, the extant tribe of Neotropical emballonurids, most species of which do not roost in caves as discussed above. The fossil record of emballonurids in Florida suggests an ecological shift in the roosting preferences of New World emballonurids through time, from cavernicolous species in the Oligocene to tree-roosting (non-cave dwelling) species in the Miocene and continuing to the present with the predominance of tree-roosting species in the modern Neotropical fauna.

The late Oligocene and Miocene emballonurid fossils from South America, including samples from La Venta, Colombia and Contamana, Peru, were preserved in sediments derived from fluvial, lacustrine, or tropical forest environments, not karst deposits (Czaplewski, 1997, 2005; Antoine et al., 2016). Only one of the South American Tertiary emballonurids has been identified below the family level, the extant genus *Diclidurus* from the middle Miocene La Venta Fauna (Czaplewski, 1997). The living species *Diclidurus albus* roosts in tropical vegetation, especially where palm trees are abundant (Ceballos and Medellín, 1988). In this species, which has white fur, sunlight filtered through the palm leaves on white fur gives the fur a greenish cast and provides a form of camouflage in the roost or in flight (as it does for the white phyllostomid bat, *Ectophylla alba* and other species; Brooke, 1990; Rodríguez-Herrera et al., 2007; Rydell et al., 2019).

The occurrence of four species of Emballonuridae in the Oligocene and early Miocene of Florida also has paleoclimatic implications. The Emballonuridae is a tropical family of bats. The present distribution of emballonurid species in the New World closely tracks the occurrence of tropical forests, which also defines the northern limits of the Neotropical Region (Olson et al., 2001). Several species of living emballonurids, in particular *Balantiopteryx plicata*, occur at the northern edge of the Neotropics in Mexico, as far north as the Tropic of Cancer (~23° North) in the lowlands of eastern Mexico and somewhat farther north (~27° N) along the Pacific coast of western Mexico (Simmons, 2005). The approximate latitudes of the Florida Oligocene and early Miocene emballonurid records are somewhat farther north than the northernmost current Mexican records of species in this family: Brooksville 2 (28° N), I-75 (29° N), and Thomas Farm and Buda (30° N). No emballonurids are known from the modern fauna of Florida, or from Florida fossil sites younger than the early Miocene Thomas Farm LF.

The disappearance of emballonurids from Florida after the early Miocene reflects the overall trend in Florida Tertiary chiropteran faunas. Oligocene bat faunas (~24–30 Ma) are dominated by families now primarily tropical in distribution, in particular the Emballonuridae and Mormoopidae, but also including the Natalidae and Molossidae (Czaplewski et al., 2003a; Morgan and Czaplewski, 2003, 2012). The Vespertilionidae, widely distributed in temperate regions at present, is represented by a single tooth in the early Oligocene I-75 LF and is absent from the late Oligocene Brooksville 2 LF (Morgan and Czaplewski, 2012). Two indeterminate species of vespertilionids were reported from the late Oligocene White Springs LF in northern peninsular Florida (Morgan and Czaplewski, 2012). White Springs is a non-karst deposit consisting of shallow marine and fluvial sediments that, in addition to marine vertebrates (sharks, rays, bony fish, sirenians), also contains a rather diverse land mammal fauna, including two species of bats, seven species of rodents, several partial articulated skeletons of the oreodont *Mesoreodon floridensis*, and other mammals indicative of an early late Arikareean age (Ar3; MacFadden and Morgan, 2003). A latest Oligocene age for White Springs is supported by a strontium isotope age estimate of 24.4 Ma on marine mollusk shells from the same unit that produced the land mammal fauna (Jones et al., 1993).

The early Miocene (~18 Ma) Thomas Farm LF also contains three families of tropical bats, Emballonuridae, Natalidae, and Molossidae, but the overall fauna is dominated (>90% of fossil sample) by the more temperate Vespertilionidae, including at least five species (Lawrence, 1943; Czaplewski and Morgan, 2000; Czaplewski et al., 2008; Morgan and Czaplewski, 2012). The chiropteran record in Florida between the early Miocene and early Pleistocene (~2-18 Ma) is sparse; only a few fossils are known almost all of which are vespertilionids (Morgan and Hulbert, 2008; Morgan and Czaplewski, 2012). Changes in the distributional patterns of Florida bats during the mid Cenozoic almost certainly reflect overall climatic changes in the Florida peninsula and southeastern North America, from a tropical or subtropical climate in the Oligocene and early Miocene to a warm temperate climate from the middle Miocene to the present.

A diverse middle Miocene paleoflora from the Florida Panhandle provides information on the vegetation and climate of Florida during the time period shortly after the early Miocene Thomas Farm LF. Jarzen et al. (2010) reviewed the palynology and Lott et al. (2019) reviewed the macroplant remains from the Alum Bluff flora in the Fort Preston Formation along the Apalachicola River in the central Florida Panhandle (Latitude: 30°28’N). The Alum Bluff flora has been dated as middle Miocene (early Barstovian NALMA; ~16 Ma) based on an associated land mammal fauna consisting of four taxa of ungulates, as well as molluscan biostratigraphy and strontium isotope chronology of underlying and overlying marine units (Bryant et al., 1992). The two paleobotanical studies documented that the affinities of many of the identified palynomorphs and macroplants from the Alum Bluff flora indicate a warm temperate climate, much like that found in the northern Gulf Coast region of Florida today. The plant community consisted of an elm (*Ulmus*)–hickory (*Carya*)–palm forest (*Sabalites*- an extinct genus near the modern sabal or cabbage palm *Sabal*), occurring in close proximity to an oak and pine-dominated landscape. This interpretation of the Alum Bluff flora is much different from a previous study more than a century earlier that interpreted this same flora as being tropical to subtropical in its affinities (Berry, 1916). The Alum Bluff flora closely resembles the modern floras of the northern Gulf Coast through the north-central and northern Atlantic coast regions of peninsular Florida and extending northward along the Atlantic coasts of Georgia and South Carolina. The results of a climate analysis of the Alum Bluff flora, using leaf margin and leaf area (Lott et al., 2019), gave estimates of 19°C mean annual temperature and 116 cm mean annual precipitation, both of which are similar to modern values of mean annual temperature and precipitation for the Florida Panhandle and the north-central Florida peninsula.

No Oligocene or early Miocene paleofloras are known from Florida. An attempt to recover pollen from the early Miocene Thomas Farm site was unsuccessful (Pratt, 1989, 1990). The presence of tropical bats in Oligocene and early Miocene vertebrate faunas from peninsular Florida provides a proxy for the mid Cenozoic climate and vegetation in this region. The prevalence of tropical families of bats in Florida Oligocene faunas (~24–30 Ma) is indicative of a tropical to subtropical climate and vegetation during this time period. In the early Miocene Thomas Farm LF, the predominance of the more temperate family Vespertilionidae, together with the uncommon occurrence of three families of primarily tropical bats, suggests that the climate had moderated by the late early Miocene (~16–18

Ma), with subtropical habitats and vegetation predominating. Based on the modern fauna, emballonurids in the New World are a particularly sensitive indicator of tropical forest habitats. The diclidurine emballonurid *Floridopteryx* would seem to indicate the presence of subtropical habitats, or perhaps even small pockets of tropical vegetation, in the vicinity of the Thomas Farm sinkhole in the early Miocene. With the transition to a more temperate climate in the middle Miocene, as indicated by the warm temperate Alum Bluff flora, tropical groups of bats disappeared from Florida presumably because of the disappearance of tropical and/or subtropical vegetation and habitats.

Similar mid Cenozoic changes are also observed in the European chiropteran fauna, transitioning from a tropical or subtropical fauna in the Eocene, Oligocene, and early Miocene to a temperate fauna after the middle Miocene (Legendre, 1980; Sigé and Legendre, 1983; Horáček, 2001; Gunnell and Simmons, 2005). Two genera of emballonurids are known from the middle Eocene of Europe, *Tachypteron* and *Vespertiliavus*, and *Vespertiliavus* also occurs in late Eocene and early Oligocene European faunas. A record of the extant genus *Taphozous* from the early Miocene is the youngest emballonurid from Europe (Legendre, 1980; Gunnell and Simmons, 2005). Vespertilionids underwent an expansion and diversification in European faunas during the Miocene (Sigé and Legendre, 1983; Horáček, 2001; Gunnell and Simmons, 2005), much as they did in the Miocene of Florida and elsewhere in North America (Czaplewski et al., 2008; Morgan and Czaplewski, 2012), and presumably for the same reason, the cooling climate and expansion of temperate habitats in the Northern Hemisphere.

Tropical species of bats are unknown from fossil deposits in the Florida peninsula after the early Miocene, except for a brief appearance of several species in the Pleistocene, including (Morgan et al., 1988; Morgan, 1991, 2002): two species of Phyllostomidae, the vampire bats *Desmodus archaeodaptes* and *D. stocki*, both now extinct; two species of Mormoopidae, the extant *Mormoops megalophylla* and the extinct *Pteronotus* cf. *pristinus*; and a large living species of Molossidae, *Eumops underwoodi*. Among these Pleistocene bats with Neotropical affinities, three species are extinct and the extant species *M. megalophylla* and *E. underwoodi* are currently extralimital to Florida, occurring no closer than the southwestern U. S. and northern Mexico. Morgan and Emslie (2010) attributed the occcurrence of tropical/subtropical bats in Florida Pleistocene faunas, as well as other species of mammals and birds with tropical affinities, to changes in climate, vegetation, and biogeographic patterns during glacial and interglacial periods, beginning at about 2.6 Ma and continuing to the end of the Pleistocene.

The modern chiropteran fauna of Florida consists of 20 species, mainly composed of Vespertilionidae (13 species), together with seven species belonging to two other families with tropical affinities, the Molossidae and Phyllostomidae (Marks and Marks, 2006). Three species of molossids are recorded from the modern Florida fauna, the widespread Brazilian or Mexican free-tailed bat *Tadarida brasiliensis*, the Florida bonneted bat *Eumops floridanus* from southern peninsular Florida, and the velvety free-tailed bat *Molossus molossus* from the Florida Keys (Frank, 1997b; Marks and Marks, 2006). *Eumops floridanus* is endemic to the southern half of the Florida peninsula (Koopman, 1971; Timm and Genoways, 2004; Vannatta et al., 2021), and also has been identified from three late Pleistocene fossil deposits in southern Florida (Morgan, 1991, 2002). In fact, *E. floridanus* was originally described as the extinct species *Molossides floridanus* based on a mandible from the late Pleistocene Melbourne LF in Brevard County about midway along the Atlantic Coast of Florida (Allen, 1932), before it was discovered as a living animal in Miami at the southern tip of the peninsula (Barbour, 1936; Koopman, 1971). The Melbourne LF is slightly north of the currently known range of *E. floridanus* (Vannatta et al., 2021). The biogeographic origin of *E. floridanus* appears to be from the West Indies, as genomic data indicate this species is very similar to *E. ferox* from Cuba (Timm and Genoways, 2004; McDonough et al., 2008; Bartlett et al., 2013). Four species in the Phyllostomidae, the West Indian fruit bat *Artibeus jamaicensis*, the Cuban fig-eating bat *Phyllops falcatus*, the buffy flower bat *Erophylla sezekorni*, and the Cuban flower bat *Phyllonycteris poeyi*, are West Indian bats known in Florida only by rare records from the Florida Keys (Frank, 1997a; Marks and Marks, 2006). The records of the four phyllostomids from the Florida Keys almost certainly represent accidental occurrences from Cuba, probably during hurricanes.

Biogeography and Evolutionary History of the Emballonuridae

The Emballonuridae is a pantropical family of bats found in Mesoamerica, South America, Africa, Southeast Asia, Australia, and some Pacific Islands (Simmons, 2005; Simmons and Cirranello, 2019). There are 14 genera and over 50 species of extant Emballonuridae (Simmons, 2005; Goodman et al., 2012; Simmons and Cirranello, 2019): six genera in the Old World (*Coleura*, *Emballonura*, *Mosia*, *Paremballonura*, *Saccolaimus*, and *Taphozous*) and eight genera in the New World (*Balantiopteryx*, *Centronycteris*, *Cormura*, *Cyttarops*, *Diclidurus*, *Peropteryx Rhynchonycteris*, and *Saccopteryx*). The geographic occurrence of the six genera of Old World emballonurids is as follows: *Saccolaimus* and *Taphozous* have similar distributions, occurring in Africa, southerm Asia, and Australia; *Coleura* is restricted to Africa, Madagascar off the east coast of Africa, and the Seychelles in the Indian Ocean; *Emballonura* is found in southeast Asia and the Pacific Islands; *Paremballonura* is known from two species in Madagascar; and the single species of *Mosia* occurs in eastern Indonesia, New Guinea, the Bismarck Archipelago, and the Solomon Islands.

Most genera of New World emballonurids have a widespread distribution in the Neotropical region, occurring from southern Mexico or northern Central America south throughout Central America and the tropical portion of South America, with at least one species found as far south as Paraguay (Simmons, 2005; Lopez-Aguirre et al., 2019; Simmons and Cirranello, 2019). Their occurrence mirrors the distribution of tropical forests. The northernmost New World emballonurid, *Balantiopteryx plicata*, occurs as far north as southern Sonora and southern Chihuahua in northwestern Mexico (~27° N; Alvarez-Castañeda and Patton, 1999) and eastern San Luis Potosí in eastern Mexico (~22° N; López-Forment and Tellez-Giron, 2014). Five other species of emballonurids, *Balantiopteryx io*, *Diclidurus albus*, *Peropteryx macrotis*, *Rhynchonycteris naso*, and *Saccopteryx bilineata*, occur in the tropical lowlands of eastern Mexico as far north as Veracruz, with several of these species found somewhat farther north in the Mexican Pacific coastal states of Guerrero, Jalisco, and Nayarit (Medellín et al., 2008; Ceballos et al., 2014). Emballonurids are absent from the West Indies, except for several continental islands in the southern Caribbean Sea that would have been connected to northern South America during the late Pleistocene low sea level stand, including Trinidad with five species of emballonurids, Tobago with three species, Margarita with two, and Aruba with a single species (Simmons, 2005). *Peropteryx trinitatis* occurs on these islands and on Grenada, an oceanic island at the southernmost end of the Lesser Antillean archipelago. All of these islands, including Grenada, have a South American chiropteran fauna lacking Antillean endemic species (Eshelman and Morgan, 1985; Koopman, 1989; Genoways et al., 1998).

The previous published fossil record of the Emballonuridae in the Western Hemisphere is sparse, even if records from late Pleistocene cave deposits are included. This is probably a result of the roosting habits of New World emballonurids, most of which are not typically found in caves (see Taphonomy and Paleoecology discussion above). Besides the Oligocene and early Miocene records from Florida described here, all other Tertiary records of New World Emballonuridae are from South America, consisting of seven isolated teeth from four different localities. Two associated upper molars referred to the living genus *Diclidurus* and a canine of a smaller indeterminate emballonurid were identified from the middle Miocene La Venta Fauna in Colombia (Czaplewski, 1997; Czaplewski et al., 2003b). Four isolated emballonurid teeth were reported from Oligocene and Miocene faunas from Contamana, Peru (Antoine et al., 2016 and supplementary data): two lower teeth from a late Oligocene (Deseadan SALMA) fauna in the Chambira Formation; and two records from the Miocene Pebas Formation, a large upper molar from an early Miocene (Colhuehuapian/Santacrucian SALMAs) fauna and a lower canine from a late Miocene (Mayoan/Chasicoan SALMAs) fauna. The emballonurid teeth from the Contamana faunas were not described and only identified to the family level.

The Quaternary record of the Neotropical Emballonuridae consists entirely of living species from cave deposits. Dalquest and Roth (1970) identified *Balantiopteryx io* from a late Pleistocene deposit in Cueva de Abra in southern Tamaulipas, northeastern Mexico (just south of the Tropic of Cancer at about 23° N). This cave is near the northern limit of the Neotropics but is somewhat north of the current northernmost occurrence of *B. io* in southern Veracruz (Hall, 1981; Alvarez-Castañeda and Patton, 1999; Medellín et al. 2008). *Peropteryx macrotis* was identified from Late Quaternary cave deposits in Loltún Cave in the Yucatán peninsula of Mexico (Arroyo-Cabrales, 1992; Arroyo-Cabrales and Polaco, 2003), within the modern range of the species. Eshelman and Morgan (1985) identified *P. macrotis* from Late Quaternary deposits in Robinson Crusoe Cave on Tobago in the southeastern Caribbean Sea. The extant *Peropteryx* from Tobago has since been referred to *P. trinitatis* (Simmons and Voss, 1998; Simmons, 2005), suggesting that the Quaternary fossils probably belong to *P. trinitatis* as well. Emballonurids are absent from the extensive fossil record of bats from Late Quaternary deposits in the West Indies, most of which are from caves (Morgan, 2001). The Quaternary record of emballonurids in South America consists of the extant *P. macrotis* from cave deposits in the states of Bahia and Minas Gerais, Brazil (Czaplewski and Cartelle, 1998; Lessa et al., 2005).

Two new species of Emballonuridae belonging to the new genus *Oligopteryx* are described here from the Oligocene of Florida, *O. floridanus* and *O. hamaxitos* from the Whitneyan I-75 LF and late early Arikareean Brooksville 2 LF, and a third new species, *Karstopteryx gunnelli*, is described from the latest Oligocene (early late Arikareean) Buda LF. These three Oligocene species represent the oldest New World records of the Emballonuridae, ranging in age from ~24-30 Ma. There are numerous earlier records of emballonurids from the Old World, including: early to middle Eocene of Algeria and Tunisia in northern Africa (*Vespertiliavus, Pseudovespertiliavus*); middle to late Eocene of Europe, primarily France and Germany (*Tachypteron*, *Vespertiliavus*); and late Eocene of Egypt (*Dhofarella*). The Emballonuridae apparently originated in the Old World (Europe or Africa) in the early to middle Eocene (Storch et al., 2002; Ravel et al., 2016), and dispersed to North America by the early Oligocene from either Europe or Asia (this paper), or from South America by way of Africa (Teeling et al., 2005; Lim 2007, 2008, 2009, 2010).

Molecular, morphological, biogeographic, and behavioral studies of modern Eastern Hemisphere and Western Hemisphere Emballonuridae (Teeling et al., 2005; Lim 2007, 2008, 2010; Lim and Dunlop 2008; Lim et al. 2008; Ruedi et al. 2012) have suggested that the New World Emballonurinae (Diclidurini) had an African origin. Teeling et al. (2005) and Lim (2007, 2008) proposed that emballonurids arrived in South America from Africa by overwater dispersal in the Oligocene between 25 and 31 Ma, at about the same time as the better-known dispersal of platyrrhine monkeys and caviomorph rodents from Africa to South America (e.g., Flynn and Wyss, 1998). More recent fossil discoveries in South America have extended the record of caviomorphs back to the early Oligocene (Arnal et al., 2019) and middle Eocene (Antoine et al., 2012; Assemat et al., 2019) and that of platyrrhines and parapithecid primates to the late Eocene and early Oligocene, respectively (Bond et al., 2015; Seiffert et al., 2020). Prior to 2010, the earliest published record of the Emballonuridae in the New World consisted of several teeth from the middle Miocene (~12 Ma) of Colombia (Czaplewski, 1997; Czaplewski et a1., 2003b). More recently, the New World record of emballonurids has been extended back into the Oligocene on both continents, with both early and late Oligocene (~24-30 Ma) samples from Florida in southeastern North America (Morgan and Czaplewski, 2012; this paper) and isolated teeth from the late Oligocene (~25 Ma) of Contamana, Peru in South America (Antoine et al., 2016). The molecular divergence dates for the basal split of the New World emballonurines of 32.5 Ma (Lim, 2007) and 30 Ma (Teeling et al., 2005) are close in age to the oldest fossils of this group from the early Oligocene of Florida and are older than the earliest emballonurid in South America from the late Oligocene of Peru.

The emballonurid *Dhofarella*, from the late Eocene Fayum deposits in Egypt in northern Africa, has been allied with emballonurines (Gunnell et al., 2008; Ravel et al., 2016). The M1 of *Dhofarella* is more similar to that of emballonurines than to other Eocene emballonurids or extant taphozoines, and Gunnell et al. (2008) noted that *Dhofarella* is similar to the extant African emballonurine genus *Coleura*. *Dhofarella* is also known from an early Oligocene fauna from Oman on the Arabian Peninsula, which is a part of the African-Arabian continental tectonic plate, although colliding with Eurasia beginning in the late Eocene (Sigé et al., 1994). There are two other Tertiary occurences of emballonurines in Africa after the late Eocene and early Oligocene records of *Dhofarella*, including the recently described middle Miocene emballonurine *Afrillonura namibensis* from Namibia in southwestern Africa (Rosina and Pickford, 2021) and an extinct species in the extant emballonurine genus *Coleura*, *C. muthokai*, from the Pliocene of Ethiopia (Wesselman, 1984). There are also several records of taphozoine emballonurids from the Miocene and Pliocene of Africa (Gunnell and Simmons, 2005; Gunnell, 2010; Rosina and Pickford, 2019, 2020; Gunnell and Manthi, 2020). Our morphological analysis suggests that *Oligopteryx* from the Oligocene of Florida is more similar dentally to living New World emballonurines than is *Dhofarella* of equivalent age.

South America and Africa are currently separated by a minimum distance of about 2,500 km, although taking into account seafloor spreading from the Eocene to the present, this distance would have been considerably less when monkeys and rodents (and possibly bats) dispersed westward across the Atlantic. Emballonurids are certainly capable of long-distance dispersals over water, as their colonization of many Indian Ocean and Pacific Ocean islands attests. The failure of emballonurids to similarly colonize the West Indian islands is an enigma. An African origin for the New World Emballonuridae would require two oceanic dispersal events for this group, first from Africa to South America and then from South America to North America, both of which must have occurred prior to the early Oligocene (~30 Ma) record of *Oligopteryx* in Florida. Lim (2009) hypothesized that emballonurids reached Florida by overwater dispersal in the Oligocene from South America across the West Indies. The absence of emballonurids in both the modern and fossil record of the West Indies suggests the more likely overwater dispersal route from South America, if indeed the New World emballonurids reached South America first (see alternate hypothesis below), was northward across the Central American Seaway (CAS), and then overland through Mesoamerica and around the western margin of the Gulf of Mexico to Florida.

Lim (2010) further elaborated upon the colonization of South America by emballonurids with a model for the diversification of the monophyletic Neotropical diclidurines, proposing an early split of the two subtribes about 27 Ma with Saccopterygina as primarily forest-adapted and Diclidurina as primarily savanna-adapted. He suggested that after a period of stasis, a rapid diversification of genera began in the early Miocene, spurred by a forest-savanna mosaic resulting from a marine incursion into the western Amazon (Lim, 2010), with the appearance of the eight modern New World genera in the early to middle Miocene between 14 and 19 Ma. The extinct diclidurine genus *Floridopteryx* is known from the early Miocene (~18 Ma) during the time interval when Lim (2010) proposed the modern genera of diclidurines evolved. The earliest record of an extant genus of diclidurine is *Diclidurus*, which first appeared at the end of this time interval in the middle Miocene (~12 Ma) of Colombia. Generic differentiation within the Diclidurini is presumed to have occurred primarily in

South America (Lim, 2008), or a New World familial differentiation in Mesoamerica and northern South America (López-Aguirre et al., 2019). The small sample of isolated teeth of emballonurids from the late Oligocene and Miocene of Contamana, Peru and middle Miocene of La Venta, Colombia (Czaplewski, 1997; Czaplewski et al., 2003b; Antoine et al., 2016) are not complete enough to evaluate Lim's hypothesis of emballonurid diversification, which was based on inferences from data on modern specimens. It is also possible with a North American (instead of African) orgin, that some of the modern genera of emballonurids had already appeared in tropical Mesoamerica in the Miocene prior to their dispersal to South America. Only a Tertiary fossil record of emballonurids from Mexico or Central America will answer this question.

López-Aguirre et al. (2019) used evidence from geographic patterns of phylogenetic diversity and phylogenetic endemism of the extant genera and species of Emballonuridae, in comparison with those of other families of bats, to confirm a hypothesis that niche conservatism limited the spread of emballonurids beyond a proposed tropical to intertropical center of origin. They also found an unusual, spatially discontinuous clustering of some emballonurid clades in certain parts of Central America with others in distant parts of South America that might indicate "in situ diversification of vicariant species, phylogenetically distant from other co-occurring species" (López-Aguirre et al., 2019, p. 1196). The Florida fossils described here fall completely outside of the family's modern Western Hemisphere distribution (as mapped by López-Aguirre et al., 2019), and thus they shed new light on the family's evolutionary biogeographic radiation in southeasternmost North America in the late Oligocene-early Miocene. The mid Cenozoic occurrence of emballonurids in the Florida peninsula probably affected the family's later patterns of diversification and endemism to an unknown degree, unless the Florida fossils were members of a clade that became extinct without giving rise to any still-living descendants.

We propose an alternative hypothesis for the origin of the New World Emballonuridae based on the available fossil evidence, which includes the presence of three extinct genera and four extinct species in this family in Florida from the early Oligocene through the early Miocene, between about 30 and 18 million years ago. We suggest that *Oligopteryx* from the early Oligocene of Florida was derived from a basal Old World emballonurid, a bat similar to *Vespertiliavus* from the Eocene of Europe, that gave rise to both the Old World (Emballonurini) and New World (Diclidurini) emballonurines. *Dhofarella* appears to be too different dentally to be closely related to *Oligopteryx*. An ancestral emballonurid dispersed to North America using either a western route from Europe across the Canadian Arctic, or possibly from eastern Eurasia across Beringia, sometime in the middle to late Eocene, giving rise to *Oligopteryx* from the early Oligocene of Florida. The western European route is perhaps more plausible, because primitive emballonurids are well known from the Eocene and Oligocene of Europe but are unknown from the Tertiary of Asia (Gunnell and Simmons, 2005). Moreover, a diverse fauna of early Eocene (Wasatchian NALMA) vertebrates, including many tropical species, is known from Ellesmere Island in the eastern Canadian High Arctic region near Greenland (McKenna, 1975; Dawson, 1976; 1991; Estes and Hutchison, 1980; Eberle and McKenna, 2002). Although the Ellesmere Island fauna is older than the earliest known emballonurid from Europe (middle Eocene), this fauna confirms that tropical vertebrates occurred in the eastern Arctic during the Eocene and that this region was on a dispersal route for Eocene vertebrates between Europe and North America.

We hypothesize that sometime prior to the late Oligocene appearance of emballonurids in Amazonian Peru, an ancestral diclidurine similar to *Oligopteryx* (but having lost the p3) dispersed southward from Central America overwater across the Central American Seaway (CAS) to the then-island continent of South America. The CAS separating North America and South America may have been as narrow as 200 km in the early Miocene at about 20 Ma (Montes et al., 2012), which was far less than the distance across the Atlantic Ocean separating South America from Africa at this same time. *Floridopteryx* from the early Miocene of Florida was derived from *Oligopteryx* or a similar genus such as *Karstopteryx*, and probably evolved in southeastern North America. Emballonurids disappeared from temperate North America (e.g., Florida) after the early Miocene but probably continued to inhabit tropical Mesoamerica, although the family has no fossil record in Mexico or Central America prior to the late Pleistocene. Emballonurids are known from Colombia and Peru from the late Oligocene to the late Miocene, between about 25 and 10 million years ago (Czaplewski, 1997; Czaplewski et al., 2003b; Antoine et al., 2016), but are unrecorded in South America between the late Miocene and late Pleistocene. Surely, the absence of emballonurids from tropical regions of both North America and South America from the late Miocene to the late Pleistocene is a collecting bias, considering the overall rarity of pre-late Pleistocene fossil deposits containing bats in the New World tropics. Bats are known from two early Miocene faunas in Panama, but no emballonurids were reported (Morgan et al., 2013).

Based on the information in the previous paragraphs, there are two conflicting hypotheses for the origin of the Neotropical Emballonuridae. The fossil evidence presented here suggests the possibility that an ancestral emballonurid from Eurasia dispersed overland to North America in the Eocene, with subsequent overwater dispersal of an ancestral emballonurine southward from tropical North America across the CAS to South America prior to the late Oligocene. A second hypothesis based primarily on molecular data from modern emballonurids proposed an Oligocene (more likely Eocene) overwater dispersal of emballonurids from Africa to South America across the Atlantic Ocean (Teeling et al., 2005; Lim, 2007, 2009), which would also require a subsequent overwater dispersal across the CAS from South America to North America prior to the early Oligocene. A phylogenetic analysis of the New World Emballonuridae indicates that all living Neotropical members of this family form a monophyletic group, the tribe Diclidurini, within the subfamily Emballonurinae (Lim, 2007; Lim et al., 2008). The two reported genera of Miocene emballonurids from the New World belong to the Diclidurini, the extinct genus *Floridopteryx* from the early Miocene of Florida and the somewhat younger record of the extant genus *Diclidurus* from the middle Miocene of Colombia (Czaplewski, 1997; Czaplewski et al., 2003b; this paper). Dental morphology indicates that *Oligopteryx* from the Oligocene of Florida may be a basal diclidurine, although we do not formally refer this extinct genus to a subfamily or tribe within the Emballonuridae.

It is also possible that the Emballonuridae from North America and South America had a dual origin, from Eurasia and Africa, respectively, and that only the South American diclidurines survived and the North American members of the family became extinct after the early Miocene. Based on this hypothesis, the Oligocene and Miocene emballonurids from Florida and the Oligocene, Miocene, and modern emballonurids from South America would not be monophyletic. However, our morphological analysis suggests the New World emballonurines are monophyletic (Tribe Diclidurini), with *Floridopteryx* being a member of the Diclidurini and *Oligopteryx* basal to the Diclidurini if not a member of this tribe. The known South American Tertiary emballonurid fossils are very fragmentary, consisting entirely of isolated teeth, and as such provide little information pertaining to the phylogeny or monophyly of New World emballonurids.

Additional information from the fossil record is required before we can fully understand the evolutionary history of the Emballonuridae in the New World, specifically if the Neotropical members of this family (tribe Diclidurini) had an African or Eurasian origin or possibly a more complicated dual origin. Over the past several decades, discoveries of Oligocene and Miocene emballonurids in both North America (Florida) and South America (Colombia and Peru) have greatly improved our knowledge of the fossil history of this family in the New World. Future discoveries of emballonurid fossils in Oligocene or older sites in North America and/or South America should provide additional data on the antiquity of this family in the Western Hemisphere and its possible origin(s).

Brief Evolutionary History of New World Noctilionoidea, Molossidae, and Vespertilionidae

The fossil record and evolutionary history of several other families of New World bats are pertinent to a better understanding of the origin and biogeography of the Neotropical Emballonuridae. In addition to the Emballonuridae, three other families of bats, Phyllostomidae, Molossidae, and Vespertilionidae, occurred in both North America and South America prior to the onset of the Great American Biotic Interchange in the late Miocene (~9 Ma). An undescribed new genus of phyllostomine phyllostomid occurs in two early Miocene faunas (~18-21 Ma) in Panama in southernmost North America (Morgan et al., 2013) and an indeterminate phyllostomine was identified from a fauna of similar early Miocene age (~21 Ma) from Argentina in southern South America (Czaplewski, 2010). Four phyllostomids are known from the middle Miocene La Venta Fauna in Colombia (Czaplewski, 1997; Czaplewski et al., 2003b): an extinct genus and two extinct species of large phyllostomines, *Notonycteris magdalenensis* and *N. sucharadeus*; a smaller phyllostomine similar to the genera *Tonatia* and *Lophostoma*; and the lonchophylline nectar bat *Palynephyllum antimaster*. Simmons et al. (2020) noted a p3 of late Miocene age (Mayoan SALMA; ~11 Ma) from Contamana, Peru that appears to belong to a species in the phyllostomid subfamily Stenodermatinae but was identified as the primate *Cebuella* sp. by Marivaux et al. (2016). This tooth needs to be studied and confirmed but would constitute the oldest fossil record of a fruit-eating stenodermatine bat. The only other pre-late Pleistocene records of phyllostomids from South America are two recently reported humeri of the vampire bat genus *Desmodus*, one each from Uruguay and Venezuela (Ubilla et al., 2019; Czaplewski and Rincon, 2020). The precise age of these two faunas is unclear but they are either late Pliocene or early Pleistocene. Besides the two early Miocene phyllostomine records from Panama, the only other pre-late Pleistocene phyllostomids from North America are post-Interchange records of *Desmodus* from the early Pleistocene of Florida, including the latest Blancan Inglis 1A LF and early Irvingtonian Haile 16A and Haile 21A LFs (Morgan et al., 1988).

A similar evolutionary history to that of the New World Emballonuridae has been proposed for the chiropteran superfamily Noctilionoidea that includes five extant endemic Neotropical families, Phyllostomidae, Mormoopidae, Noctilionidae, Furipteridae, and Thyropteridae, as well as the extinct family Speonycteridae from the Oligocene of Florida (Czaplewski and Morgan, 2012) and the Mystacinidae from the Miocene to modern fauna of New Zealand and the Oligocene and Miocene of Australia (Hand et al., 2005). Most previous hypotheses have proposed a Gondwanan origin for the Noctilionoidea, when Australia, Africa, and South America were connected through Antarctica, as recently as the late Eocene (Hand et al., 2005; Teeling et al., 2005; Gunnell et al., 2014). Gunnell et al. (2014) suggested that noctilionoids reached South America through a series of dispersal events from Australia across Antarctica. The main difference between the proposed evolutionary histories for the New World Emballonuridae and Noctilionoidea is that the emballonurids are thought to have been derived from Africa (Teeling et al., 2005; Lim, 2007, 2010), whereas noctilionoids had an Australian origin (Hand et al., 2005; Gunnell et al., 2014). As with the Emballonuridae, a North American/Eurasian origin has also been proposed for the Noctilionidea, based on the occurrence of the oldest known members of this superfamily in the Oligocene of Florida, consisting of an extinct genus and species in the Mormoopidae and the extinct family Speonycteridae (Czaplewski and Morgan, 2012; Morgan et al., 2019). The oldest member of the extant family Mormoopidae, the extinct genus and species *Koopmanycteris palaeomormoops* (Morgan et al., 2019), and two species in the extinct genus *Speonycteris*, *S. aurantiadens* and *S. naturalis*, in the extinct basal noctilionoid family Speonycteridae, have been described from the same two faunas in Florida that produced *Oligopteryx flori-*

danus and *O. hamaxitos*, the early Oligocene I-75 LF and the late Oligocene Brooksville 2 LF. If the Noctilionoidea and Emballonuridae first dispersed to South America from either Africa or Australia via Antarctica, then their occurrence in the early Oligocene of Florida would require pre-Oligocene fossils of both groups from South America (neither of which are known that early from the continent) and two separate pre-Oligocene overwater dispersal events, first from Africa or Australia/Antarctica to South America and then from South America to North America across the CAS.

Species in the Molossidae occur in Oligocene and Miocene faunas in both North America and South America. Molossids have been identified in eight Tertiary faunas in South America, including four described species in two genera: three extinct species in the extant genus *Mormopterus, M. faustoi* from the late Oligocene Tremembé Fauna in Brazil, *M. barrancae* from the early Miocene Gran Barranca Fauna in Argentina, and *M. colombiensis* from the middle Miocene of La Venta, Colombia; and the extinct genus and species *Potamops mascahehenes* from La Venta (Paula Couto, 1956; Czaplewski, 1997, 2010; Czaplewski et al., 2003b). An indeterminate species of the extant molossid genus *Eumops* is known from La Venta, and there are also several South American records of Eocene, Oligocene, and Miocene molossids that were not identified below the family level (Czaplewski, 1996a, 1997, 2010; Czaplewski et al., 2003b; Antoine et al., 2016; Czaplewski and Campbell, 2017).

North American Tertiary Molossidae are known from seven faunas, only one of which has been formally described. The oldest known molossid is from North America, *Wallia scalopidens* from the middle Eocene (Uintan NALMA) of Swift Current Creek, Saskatchewan, Canada (Storer, 1984; Legendre, 1985), although Smith et al. (2012) considered the familial status of *Wallia* uncertain pending the discovery of more complete specimens. The Swift Current Creek Fauna is 42-44 Ma in age (Storer, 1984), whereas the earliest molossid from the Old World, *Cuvierimops* from the late Eocene of France, is slightly younger at about 39 Ma (Legendre, 1985; Maitre, 2014). Antoine et al. (2016) listed lower teeth of a molossid from an early middle Eocene (Barrancan SALMA; 41-42 Ma) fauna in Contamana, Peru, but did not illustrate or describe these specimens. Czaplewski et al. (2003a) described and illustrated an upper molar of an indeterminate genus of molossid from the late Oligocene Brooksville 2 LF and upper molars of two distinct species similar to *Tadarida* or *Mormopterus* from the early Miocene Thomas Farm, none of which were named. Several lower jaws and partial humeri of an unidentified molossid were reported from the early Miocene (early Hemingfordian) Miller site in Florida (Morgan and Czaplewski, 2012). There are three records of molossids from post-Interchange late Pliocene (Blancan) faunas in North America: a lower premolar from the Deer Park LF in Kansas (Czaplewski et al., 2018) and a distal humerus from the Macaphalt Shell Pit LF in southern peninsular Florida (Czaplewski et al., 2003a), both referred to the extant genus *Tadarida*; and an M3 tentatively referred to the extant species *Eumops perotis* from the McRae Wash LF in Arizona (Czaplewski (1993). *Eumops* also occurs in the middle Miocene of Colombia suggesting a South American origin for this genus.

Bats similar to or congeneric with *Tadarida* are known from the early Miocene of Florida but are unknown from pre-late Pleistocene faunas in South America, indicating a northern (North American or Eurasian) origin for this genus. *Tadarida* is also known from Oligocene through the present in Europe (Gunnell and Simmons, 2005; Simmons, 2005). Because of the widespread occurrence of molossids in Tertiary faunas in North America, South America, and the Old World (Gunnell and Simmons, 2005), as well as the lack of a well-constrained phylogeny that includes both living and extinct members of this family, it is premature to propose an evolutionary history for the New World members of this group. An African, Eurasian, or North American origin are all possible, and a dual origin for certain groups within the family is also a possibility. Further studies of modern and fossil molossids in both North and South America, as well as the recovery of additional fossils, are necessary before we can develop a better understanding of the fossil history of this family in the Western Hemisphere.

Czaplewski et al. (2003b) tentatively identified the first member of the Vespertilionidae from the Tertiary of South America, based on a lower molar from the middle Miocene La Venta Fauna in Colombia. The Vespertilionidae is the most common family of bats in Tertiary faunas in North America (Czaplewski et al., 2008), and species of vespertilionids also dominate the modern North American chiropteran fauna (Simmons, 2005). The fossil record suggests the Vespertilionidae had a northern origin in Eurasia or North America (Gunnell and Simmons, 2005), and dispersed from North America to South America across the CAS sometime before the middle Miocene.

Four families of bats (Emballonuridae, Phyllostomidae, Molossidae, Vespertilionidae) have been recorded in both North America and South America in the middle Miocene or earlier (>12 Ma), well before the Great American Biotic Interchange began at about 9 Ma (Morgan, 2008; Woodburne, 2010). Clearly, the overwater dispersal capabilities of bats are greater than those of non-volant mammals, and as such bats should be evaluated separately when discussing mammals and the GABI. North America and South America were not known to share a single family of non-volant mammals prior to late Miocene onset of the GABI, until recently when Bloch et al. (2016) described the cebid monkey *Panamacebus transitus* from the early Miocene (late Arikareean) Lirio Norte fauna in Panama, the southernmost extension of North America in the Miocene. Tertiary fossils of platyrrhine primates, and specifically the family Cebidae, were previously known only from South America. The Lirio Norte fauna and the somewhat younger early Miocene (early Hemingfordian) Centenario Fauna, both from the Panama Canal area, also produced an as-yet-undescribed new genus of phyllostomid bat, another group previously thought to have been confined to South America before the Interchange (Morgan et al., 2013). Both the Lirio Norte and Centenario faunas also contain vertebrae of the boid snake *Boa* of South American origin (Head et al., 2012). Early Miocene deposits from Panama have produced a diverse paleoflora with strong South American or Gondwanan affinities (Jaramillo et al., 2014). The Panama fossils confirm that an interchange of vertebrates and plants occurred between the tropical regions of North America and South America in the early Miocene (~18–21 Ma), when the two continents were separated by a seaway that may have been as narrow as 200 km (Montes et al., 2010), long before the beginning of the better-known GABI. Other than the cebid monkey, phyllostomine bat, boid snake, and a few species of freshwater reptiles, including several turtles and a caiman, almost all other vertebrates from the Lirio Norte and Centenario faunas are North American in origin. These two Panamanian early Miocene faunas contain a diverse assemblage of large mammals with North American affinities including amphicyonid (Amphicyonidae) and procyonid (Procyonidae) carnivorans, horses (Equidae), rhinos (Rhinocerotidae), chalicotheres (Chalicotheriidae), peccaries (Tayassuidae), anthracotheres (Anthracotheriidae), oreodonts (Oreodontidae), camels (Camelidae), and protoceratids (Protoceratidae), as well as three North American families of rodents, the extinct Jimomyidae and the extant Sciuridae and Heteromyidae (MacFadden et al., 2014; Bloch et al., 2016).

TERTIARY FOSSIL RECORD OF THE NEOTROPICAL CHIROPTERA: AN UPDATE

This contribution is the last paper in a series describing six new genera and eight new species of Oligocene and Miocene bats from Florida belonging to four families with tropical affinities. Two of these are extant families now endemic to the New World tropics (Mormoopidae, Natalidae), one is an extant family with a pantropical distribution (Emballonuridae), and one is an extinct family (Speonycteridae) belonging to the superfamily Noctilionoidea that also includes five living families endemic to the Neotropics (Morgan and Czaplewski, 2003; Czaplewski and Morgan, 2012; Morgan et al., 2019; this paper).

We present an update of our review from a decade ago of the Tertiary fossil record of New World bats with tropical affinities (Morgan and Czaplewski, 2012). Although we realize this discussion includes some repetition from previous sections of this paper, our intention is to provide a comprehensive, stand-alone status report of the Tertiary chiropteran fauna with Neotropical affinities from the Western Hemisphere. These records include not only localities within the modern Neotropical biogeographic region, primarily from South America, but also the diverse fauna of bats with Neotropical affinities mentioned above from mid Cenozoic localities in Florida, which is located in the modern Nearctic biogeographic region. It is important to clarify here that the current biogeographic regions are based on the historic flora and fauna (Olson et al., 2001), whose ecosystems have been radically altered by the 21st century (Keith et al., 2022), and that those regions may have had quite different geographic boundaries in the geologic past. The current Neotropical region includes South America, the West Indies, Central America, and Mexico north to the Tropic of Cancer at about 23°N. The Nearctic region includes the United States, Canada, and the temperate region of northern Mexico south to the Tropic of Cancer. Prior to the Great American Biotic Interchange beginning in the late Miocene (~9 Ma), fossil evidence suggests the Neotropical region would have had very different boundaries, including the then-island continent of South America and probably the West Indies but not Mesoamerica (Mexico south to Panama) which was a tropical province of the Nearctic region at that time. As discussed above, early Miocene faunas from Panama consist primarily of North American species of mammals (MacFadden et al., 2014; Bloch et al., 2016), even though Panama's current mammalian fauna has a strong Neotropical component (Eisenberg, 1989).

Over the past three decades, our knowledge of the fossil history of the Neotropical Chiroptera has improved dramatically. Before 1990, only three named Tertiary taxa with Neotropical affinities belonging to two families (Phyllostomidae, Molossidae) had been described from the Western Hemisphere: an extinct genus and species of phyllostomine phyllostomid, *Notonycteris magdalenensis*, from the middle Miocene La Venta Fauna in Colombia (Savage, 1951); an extinct species belonging to an extant genus of molossid, *Mormopterus faustoi*, from the late Oligocene Tremembé Fauna in Brazil (Paula Couto, 1956); and the earliest known molossid, *Wallia scalopidens*, from the middle Eocene of Saskatchewan, Canada, originally named as a proscalopid mole (Storer, 1984) but later referred to the Molossidae (Legendre, 1985; also see Smith et al. 2012).

Since 1990, Tertiary fossils representing eight of the nine families of bats now inhabiting the Neotropical region have been reported, including fossils from both South America and North America. The only Neotropical bat family currently lacking a Tertiary fossil record is the Furipteridae. Most of these new paleontological discoveries are from four widely separated regions: five early Oligocene through early Miocene faunas in peninsular Florida in southeastern North America (Czaplewski et al., 2003a; Morgan and Czaplewski, 2003, 2012; Czaplewski and Morgan, 2012; Morgan et al., 2019; this paper); and three areas in South America: the middle Miocene of Colombia (Czaplewski, 1997; Czaplewski et al., 2003b); the middle Eocene through late Miocene in the western Amazon Basin of Peru and Brazil (Czaplewski, 1996a; Czaplewski and Campbell, 2004, 2017; Antoine et al., 2016); and the early Eocene and early Miocene of Patagonia in Argentina (Tejedor et al., 2005; Czaplewski, 2010).

Table 5 is a current list of all described taxa of Tertiary bats from South America and North America with Neotropical affinities, also including records identified only to the family or genus level. The location of these sites is indicated on maps of South America (Fig. 20) and North America (Fig. 21). Two Eocene records of Molossidae are included in Table 5 but otherwise Eocene bats are excluded because their systematic relationships and biogeographic affinities with modern families are not well understood. Almost all Tertiary records of bats from South America are included on this list, whereas the records from North America exclude the Vespertilionidae. The majority of post-

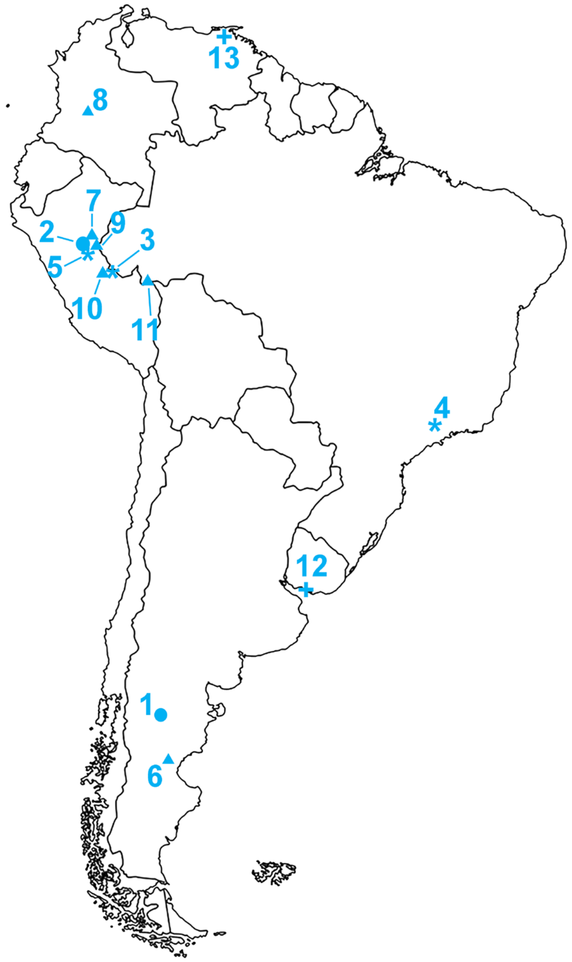

Figure 20. Tertiary sites containing bats from South America (Chiroptera: Emballonuridae, Phyllostomidae, Noctilionidae, Thyropteridae, Molossidae, Vespertilionidae). Table 4 lists the taxa of bats known from most of these sites. The sites are numbered in order from oldest to youngest. Symbols designate different epochs: Eocene (filled circle); Oligocene (asterisk); Miocene (triangle), Pliocene (plus sign). Eocene: **1.** Laguna Fría, Argentina (early Eocene), site not listed in Table 4 because the bat is not identified below the level of Chiroptera; **2.** Pozo Formation, Contamana, Peru (middle Eocene, Barrancan); Oligocene: **3.** Santa Rosa, Peru (early Oligocene), site not listed in Table 4 because the bat is not identified below the level of Chiroptera. **4.** Tremembé Formation, Brazil, (late Oligocene, Deseadan); **5.** Chambira Formation, Contamana, Peru (late Oligocene, Deseadan). Miocene: **6.** Gran Barranca, Argentina (early Miocene, Colhuehuapian); **7.** Pebas Formation, Contamana, Peru (early Miocene, Colhuehuapian/Santacrucian); **8.** La Venta, Colombia (middle Miocene, Laventan); **9.** Pebas Formation, Contamana, Peru (late Miocene, Mayoan/Chasicoan); **10.** Juruá River, Brazil (late Miocene, Huayquerian); **11.** Río Acre, Peru (late Miocene, Huayquerian). Pliocene: **12.** Kiyú, Uruguay (late Pliocene-middle Pleistocene); **13.** El Breal de Orocual, Venezuela (late Pliocene/early Pleistocene).

Eocene Tertiary bats from North America have been referred to the Vespertilionidae (Czaplewski et al., 2008), and are not included here because they mostly represent temperate bats lacking obvious Neotropical affinities. Although some extinct genera of Vespertilionidae known from North American Tertiary fossil deposits (Czaplewski et al., 2008) may be related to Neotropical vespertilionids, the phylogenetic relationships of these extinct genera are not well enough understood to determine their biogeographic origins and affinities. Several extant genera of vespertilionids identified from North American Tertiary faunas (e.g., *Eptesicus*, *Lasiurus*, *Myotis*) occur in the modern fauna of the Neotropical region in Mesoamerica and South America (Czaplewski et al., 2008).

The middle Miocene (~12–13 Ma; Laventan SALMA) La Venta Fauna in Colombia has produced the most diverse Tertiary chiropteran fauna from the Western Hemisphere, numbering 14 species, including 12 genera (nine identified genera and three indeterminate but distinct genera) and six families (Czaplewski, 1997; Czaplewski et al., 2003b; Table 4). Among the nine families of bats known from the modern fauna of South America, only three are missing from the La Venta Fauna, Furipteridae, Mormoopidae, and Natalidae. The Furipteridae lack a Tertiary fossil record as noted above, whereas the Mormoopidae and Natalidae occur in the Oligocene and/or early Miocene of North America (Florida) but are unknown in South America before the late Pleistocene (Morgan and Czaplewski, 2003; Morgan et al., 2019). More than half of the La Venta chiropteran fauna belongs to two families: four species in the Phyllostomidae, the phyllostomines *Notonycteris magdalenensis* and *N. sucharadeus*, a phyllostomine near *Tonatia* or *Lophostoma*, and the lonchophylline *Palynephyllum antimaster*; and four species in the Molossidae, *Eumops* sp., *Mormopterus colombiensis*, *Potamops mascahehenes*, and an indeterminate species distinct from the three other molossids. The other six species of bats from La Venta include: two species of Emballonuridae, *Diclidurus* sp. and a smaller indeterminate genus; one member of Noctilionidae referred to the living species *Noctilio*

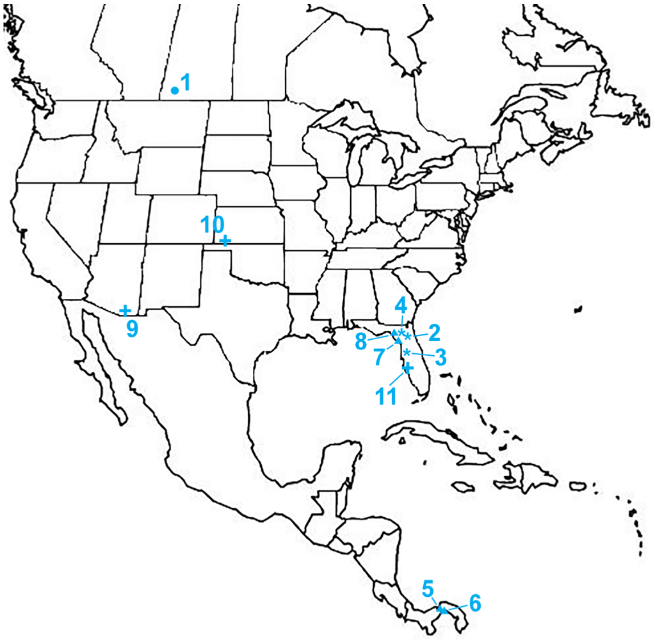

Figure 21. Tertiary sites containing bats with Neotropical affinities from North America (Chiroptera: Emballonuridae, †Speonycteridae, Phyllostomidae, Mormoopidae, Natalidae, Molossidae). Table 4 lists the taxa of bats known from each of these sites. The sites are numbered in order from oldest to youngest. Symbols designate different epochs: Eocene (filled circle); Oligocene (asterisk); Miocene (triangle), Pliocene (plus sign). Eocene: **1.** Swift Current Creek, Saskatchewan, Canada (middle Eocene, Uintan). Oligocene: **2.** I-75, Florida (early Oligocene, Whitneyan); **3.** Brooksville 2, Florida (late Oligocene, early Arikareean); **4.** Buda, Florida (latest Oligocene, late Arikareean). Miocene: **5.** Lirio Norte, Panama (earliest Miocene, latest Arikareean); **6.** Centenario, Panama (early Miocene, early Hemingfordian); **7.** Miller, Florida (early Miocene, early Hemingfordian); **8.** Thomas Farm, Florida (early Miocene, early Hemingfordian). Pliocene: **9.** McRae Wash, Arizona, (late Pliocene, Blancan); **10.** Deer Park, Kansas (late Pliocene, Blancan); **11.** Macasphalt Shell Pit, Florida (late Pliocene, Blancan).

albiventris; two species of Thyropteridae, both referred to living species, *Thyroptera lavali* and *T.* cf. *tricolor*; and an indeterminate genus and species of Vespertilionidae. La Venta is one of the most diverse Tertiary chiropteran faunas known (Gunnell and Simmons, 2005), and among the richest from a non-karst depositional environment. Two main units within the La Venta stratigraphic section have produced most of the bat fossils, the “Fish Bed” representing a lacustrine depositional environment and the “Monkey Beds” that sample a tropical forest habitat (Czaplewski, 1997).

In comparison, the most diverse Tertiary bat fauna from North America, Thomas Farm, Florida, is an early Miocene karst deposit with nine species. Sample size is not the reason for the difference in the number bat species in the two faunas, because Thomas Farm has an order of magnitude more individual bat fossils than does La Venta (Pratt, 1989; Czaplewski, 1997; Czaplewski et al, 2003b; Morgan and Czaplewski, 2003; this paper). At present, Colombia has well over 100 species of bats, whereas Florida has only 20 species (Simmons, 2005; Marks and Marks, 2006). The fossil record suggests the much higher diversity of bats in Colombia compared to Florida was also typical of Miocene faunas. This pattern reflects the well-known observation that chiropteran diversity or species richness in the tropics is far greater than in temperate regions (Hill and Smith, 1984; Nowak, 1994). La Venta is about 3° North of the Equator whereas Thomas Farm is 30° North.

The remainder of the Tertiary chiropteran record from South America is widely scattered, with records from Argentina, Uruguay, southern Brazil, the western Amazon basin in Brazil and Peru, and Venezuela, and mostly consists of small samples of isolated teeth and other fragmentary specimens (Table 5). No more than three taxa of bats are known from any of these localities. Until recently, there was only one record of an Eocene bat from South America, consisting of two teeth of an indeterminate family from the Laguna Fría site in Patagonia, Argentina of early Eocene age (M. Tejedor et al., 2005). A lower molar of a bat of indeterminate affinity from the Santa Rosa LF in Amazonian Peru was originally considered late Eocene in age (Czaplewski and Campbell, 2004), but is now thought to be early Oligocene (Seiffert et al. 2020; K. Campbell, pers. communication). A small sample of isolated bat teeth was recently reported from sediments representing a tropical rainforest habitat in the middle Eocene (Barrancan SALMA) Pozo Formation in Contamana, Amazonian Peru (Antoine et al., 2012, 2016 and supplementary data). These fossils were identified in a table in a

Table 5. Tertiary bats from South America and North America with Neotropical affinities. Pleistocene records are not included in this table. The order of families follows Simmons (2005). Within a family (subfamily for the Phyllostomidae), the genera and species are listed in alphabetical order, with undescribed or indeterminate genera at the end of the family. Extinct taxa are indicated by a dagger (†). The type locality for a species is indicated by an asterisk (*). Abbreviations: indet. (indeterminate, refers to fossils that are too incomplete for a positive identification to a higher taxonomic level than indicated below); NALMA (North American land mammal age), SALMA (South American land mammal age).

Family, genus, and species	Locality/localities and country/US state	Age and NALMA/SALMA	References
Emballonuridae			
Diclidurus species indet.	La Venta, Colombia	middle Miocene, Laventan	Czaplewski (1997) Czaplewski et al. (2003b)
†*Floridopteryx poyeri*	Thomas Farm, Florida*	early Miocene, early Hemingfordian	This paper
†*Karstopteryx gunnelli*	Buda, Florida*	latest Oligocene, late Arikareean	This paper
†*Oligopteryx floridanus*	I-75, Florida Brooksville 2, Florida*	early Oligocene, Whitneyan late Oligocene, early Arikareean	This paper
†*Oligopteryx hamaxitos*	I-75, Florida Brooksville 2, Florida*	early Oligocene, Whitneyan late Oligocene, early Arikareean	This paper
genus and species indet.[1,2]	La Venta, Colombia	middle Miocene, Laventan	Czaplewski et al. (2003b)
genus and species indet.[1,3]	Contamana, Peru Chambira Formation	late Oligocene, Deseadan	Antoine et al. (2016)
	Contamana, Peru Pebas Formation	early Miocene, Colhuehuapian-Santacrucian	Antoine et al. (2016)
	Contamana, Peru Pebas Formation	late Miocene, Mayoan-Chasicoan	Antoine et al. (2016)
†Speonycteridae[4]			
†*Speonycteris aurantiadens*	I-75, Florida Brooksville 2, Florida*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Czaplewski and Morgan (2012)
†*Speonycteris naturalis*	I-75, Florida*	early Oligocene, Whitneyan	Czaplewski and Morgan (2012)
Phyllostomidae[4]: Phyllostominae			
†*Notonycteris magdalenensis*	La Venta, Colombia*	middle Miocene, Laventan	Savage (1951) Czaplewski (1997) Czaplewski et al. (2003b)
†*Notonycteris sucharadeus*	La Venta, Colombia*	middle Miocene, Laventan	Czaplewski et al. (2003b)
Tonatia or *Lophostoma* species indet.	La Venta, Colombia	middle Miocene, Laventan	Czaplewski (1997) Czaplewski et al. (2003b)
undescribed genus and species	Lirio Norte, Panama Centenario, Panama	early Miocene, late Arikareean early Miocene, early Hemingfordian	Morgan et al. (2013)
genus and species indet.[1]	Gran Barranca, Argentina	early Miocene, Colhuehuapian	Czaplewski (2010)
Phyllostomidae: Desmodontinae			
Desmodus sp.	Kiyú, Uruguay Raigón Formation	late Pliocene/middle Pleistocene[5]	Ubilla et al. (2019)
cf. *Desmodus* sp.	El Breal de Orocual Venezuela	late Pliocene/early Pleistocene[6]	Czaplewski and Rincon (2020)
Phyllostomidae: Lonchophyllinae			
†*Palynephyllum antimaster*	La Venta, Colombia*	middle Miocene, Laventan	Czaplewski et al. (2003b)

Table 5. Cont.

Family, genus, and species	Locality/localities and country/US state	Age and NALMA/SALMA	References
Phyllostomidae: Stenodermatinae genus and species indet.[7]	Contamana, Peru Pebas Formation	late Miocene, Mayoan	Simmons et al. (2020)
Mormoopidae[4]			
†*Koopmanycteris palaeomormoops*	I-75, Florida Brooksville 2, Florida*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Morgan et al. (2019)
Noctilionidae[4]			
Noctilio albiventris	La Venta, Colombia	middle Miocene, Laventan	Czaplewski (1997) Czaplewski et al. (2003b)
†*Noctilio lacrimaelunaris*	Rio Acre, Peru*	late Miocene, Huayquerian	Czaplewski (1996a)
Thyropteridae[4]			
†*Amazonycteris divisus*	Rio Juruá, Brazil*	late Miocene, Huayquerian	Czaplewski and Campbell (2017)
Thyroptera lavali[8]	La Venta, Colombia	middle Miocene, Laventan	Czaplewski (1996b, 1997) Czaplewski et al. (2003b)
Thyroptera cf. *tricolor*	La Venta, Colombia	middle Miocene, Laventan	Czaplewski (1997)
Natalidae			
†*Primonatalus prattae*	Thomas Farm, Florida*	early Miocene, early Hemingfordian	Morgan and Czaplewski (2003)
genus and species indet.[1]	I-75, Florida	early Oligocene, Whitneyan	Morgan and Czaplewski (2003)
Molossidae			
Eumops cf. *perotis*	McRae Wash, Arizona	late Pliocene, Blancan	Czaplewski (1993)
Eumops species indet.	La Venta, Colombia	middle Miocene, Laventan Czaplewski et al. (2003b)	Czaplewski (1997)
†*Mormopterus barrancae*	Gran Barranca, Argentina*	early Miocene, Colhuehuapian	Czaplewski (2010)
†*Mormopterus colombiensis*	La Venta, Colombia*	middle Miocene, Laventan	Czaplewski (1997)
†*Mormopterus faustoi*	Tremembé, Brazil*	late Oligocene, Deseadan	Paula Couto (1956)
Mormopterus species indet.	Gran Barranca, Argentina	early Miocene, Colhuehuapian	Czaplewski (2010)
†*Potamops mascahehenes*	La Venta, Colombia*	middle Miocene, Laventan	Czaplewski (1997)
Tadarida species indet.[9]	Macasphalt Shell Pit, Florida Deer Park, Kansas	late Pliocene, Blancan late Pliocene, Blancan	Czaplewski et al. (2003a) Czaplewski et al. (2018)
Tadarida or *Mormopterus* species indet. [10]	Thomas Farm, Florida	early Miocene, early Hemingfordian	Czaplewski et al. (2003a)
Tadarida or *Mormopterus* species indet. [10]	Thomas Farm, Florida	early Miocene, early Hemingfordian	Czaplewski et al. (2003a)
†*Wallia scalopidens*	Swift Current Creek* Saskatchewan, Canada	middle Eocene (Uintan)	Storer (1984) Legendre (1985)
genus and species indet.[1,11]	Contamana, Peru Pozo Formation	middle Eocene, Barrancan	Antoine et al. (2016)
genus and species indet.[1,11]	Contamana, Peru Pebas Formation	late Miocene, Mayoan	Antoine et al. (2016)
genus and species indet.[1]	Rio Acre, Peru	late Miocene, Huayquerian	Czaplewski (1996)

Table 5. Cont.

Family, genus, and species	Locality/localities and country/US state	Age and NALMA/SALMA	References
Molossidae (cont.)			
genus and species indet.[1]	Rio Juruá, Brazil	late Miocene, Huayquerian	Czaplewski and Campbell (2017)
Vespertilionidae			
genus and species indet.[12]	La Venta, Colombia	middle Miocene, Laventan	Czaplewski et al. (2003b)

[1] Taxa listed as genus and species indet. (indeterminate) are included in this table only if they are clearly distinct from other described Tertiary members of the family. Taxa identified in the literature as genus and species indet. because of their incomplete or fragmentary condition are not included here.

[2] This taxon is much smaller than *Diclidurus*, the other emballonurid identified from La Venta, Colombia.

[3] The three records of emballonurids from Contamana, Peru listed here as genus and species indet. almost certainly represent three distinct taxa based on their difference in age.

[4] The extinct family Speonycteridae and the extant families Phyllostomidae, Mormoopidae, Noctilionidae, and Thyropteridae, as well as the Furipteridae (lacks a Tertiary fossil record), are placed in the superfamily Noctilionoidea.

[5] This record of *Desmodus* sp. from Uruguay was considered late Pliocene or early to middle Pleistocene in age (Ubilla et al., 2019). This specimen may represent one of only two Pliocene records of bats from South America. Because of the uncertainly in the age, the SALMA is not provided.

[6] This record of cf. *Desmodus* sp. from Venezuela was considered late Pliocene or early Pleistocene in age (Czaplewski and Rincon, 2020). This specimen may represent one of only two Pliocene records of bats from South America. Because of the uncertainty in the age, the SALMA is not provided.

[7] First reported as the primate *Cebuella* (Marivaux et al., 2016) but reidentified as the lower premolar of a stenodermatine phyllostomid (Simmons et al., (2020).

[8] Originally described as the extinct species †*Thyroptera robusta* but synonymized with the living species *T. lavali* by Czaplewski (1996b).

[9] These two late Pliocene records of an indeterminate species of *Tadarida* may represent the same species but consist of elements that are not comparable.

[10] These two early Miocene records of *Tadarida*/*Mormopterus* from Thomas Farm are distinct species based on a significant difference in size (Czaplewski et al., 2003a).

[11] The two records of molossids from Contamana, Peru listed here as genus and species indet. almost certainly represent two distinct taxa based on their difference in age.

[12] This is the only Tertiary record of the Vespertilionidae in South America. Numerous genera and species of vespertilionids are known from Tertiary faunas in North America (Czpalewski et al., 2008), but are not listed here because they do not have obvious Neotropical affinities.

supplementary data file and were not described or illustrated. We consider these and other identifications of bats from Contamana (see Oligocene and Miocene bats below and in Table 5) to be tentative pending further comparisons. Lower teeth identified as Molossidae from a middle Eocene fauna in Contamana would be among the earliest records of this family. A fragmentary lower tooth identified as Phyllostomidae would be by far the oldest record of this family, otherwise unknown before the early Miocene (see below), although we question whether a partial lower tooth is identifiable to the family level.

The Oligocene record of Chiroptera from South America is somewhat better than the Eocene record. Two partial skeletons of bats are known from lacustrine deposits of the Tremembé Formation of late Oligocene age (Deseadan SALMA) in the state of São Paulo in southern Brazil, including *Mormopterus faustoi*, an extinct species of an extant genus of Molossidae, and a second more complete but crushed skeleton of unknown familial affinity (Paula Couto, 1956; Mezzalira, 1966; Paula Couto and Mezzalira, 1971). Lacustrine sediments of the Chambira Formation of late Oligocene age (Deseadan) from Contamana, Peru, have produced two lower teeth of an emballonurid and an upper molar and upper and lower canines of a supposed "rhinolophoid" (Antoine et al., 2016, and supplementary data), a group otherwise unknown from the New World, unless emballonurids are considered rhinolophoids. We consider the identification of rhinolophoids from Contamana to be questionable pending further comparisons.

Compared to the Eocene or Oligocene, bats are much better known from the South American Miocene (~7–20 Ma), including 14 species from the middle Miocene of La Venta, Colombia listed above (Czaplewski, 1997; Czaplewski et al., 2003b; Table 4). Five other Miocene faunas from South America have produced bats. The early Miocene Gran Barranca Fauna (Colhuehuapian SALMA) from Patagonia in southern Argentina consists of three species (Czaplewski, 2010): a lower molar of an indeterminate genus of phyllostomine phyllostomid; a mandible with p3-m2 named as the new species *Mormopterus barrancae*; and a smaller species of *Mormopterus*. Two faunas from the Miocene Pebas Formation in Contamana, Peru have produced bats (Antoine et al., 2016 and supplementary data; Table 5): an emballonurid from an early Miocene fauna (Colhuehuapian or Santacrucian SALMA) and a different taxon of emballonurid, a molossid, and a possible stenodermatine phyllostomid (Simmons et al., 2020) from a late Miocene fauna (Mayoan or Chasicoan SALMAs). Late Miocene (Huayquerian SALMA) faunas from exposures along three rivers in the western Amazon basin in Brazil and Peru, Rio Acre, Rio Purus, and Rio Juruá, have produced bats. The only extinct species in the Noctilionidae, *Noctilio lacrimaelunaris*, was described from the Rio Acre and a small molossid of an indeterminate genus was identified from the Rio Purus, both referred to the Rio Acre Fauna from Peru (Czaplewski, 1996a). An extinct genus and species in the Thyropteridae, *Amazonycteris divisus*, was described from the Rio Juruá in Brazil, together with an isolated tooth of an indeterminate genus of molossid (Czaplewski and Campbell, 2017).

Until recently, Pliocene bats were unknown from South America. Ubilla et al. (2019) reported a possible Pliocene bat from the Kiyú site in Uruguay, a humerus of a large species of the vampire bat *Desmodus* (Phyllostomidae: Desmodontinae) The age of the fossil vampire from Uruguay is somewhat problematic, with the authors suggesting an age range between late Pliocene and middle Pleistocene (Ubilla et al., 2019). Shortly thereafter, Czaplewski and Rincon (2020) reported another humerus of a large species of *Desmodus* from the El Breal de Orocual asphaltic deposit (tar pit) in Venezuela of either late Pliocene or early Pleistocene age. Although these two *Desmodus* records from Uruguay and Venezuela may be early Pleistocene rather than Pliocene, and thus not technically Tertiary, they represent the only South American fossil records of the Chiroptera in the time interval spanning the late Miocene to the late Pleistocene. The Venezuelan record of *Desmodus* is intriguing because it is from northern South America and is similar in age to the oldest record of *Desmodus* in North America, from the early Pleistocene (latest Blancan, ~2 Ma) Inglis LF in Florida (Morgan et al., 1988). The rarity of Pliocene bats from South America hinders our ability to adequately evaluate the biogeographic history of the Neotropical chiropteran fauna. This is especially relevant because one of the most important biogeographic events in the history of the Western Hemisphere, the Pliocene to early Pleistocene (~1–5 Ma) phase of the Great American Biotic Interchange, began in the early Pliocene with the initial connection of North America and South America at the Panamanian isthmus (O'Dea et al., 2016).

The discovery of a diverse fauna of bats with tropical affinities from the Oligocene and early Miocene of Florida (Czaplewski et al., 2003a; Morgan and Czaplewski, 2003, 2012; Czaplewski and Morgan, 2012; Morgan et al., 2019; this paper), including the Emballonuridae, Mormoopidae, extinct noctilionoid family Speonycteridae, Natalidae, and Molossidae, has significantly improved the chiropteran fossil record but has also complicated the narrative regarding the New World origins and evolutionary histories of these groups. Two Oligocene bat faunas from peninsular Florida are almost entirely composed of species with Neotropical affinities, the early Oligocene (~30 Ma) I-75 LF and the late Oligocene (~26–28 Ma) Brooksville 2 LF. These two sites have been discussed in detail above as they have produced samples of a new genus and two new species of emballonurids, *Oligopteryx floridanus* and *O. hamaxitos*, described here. These two sites have similar chiropteran faunas, including (Czaplewski et al., 2003a; Morgan and Czaplewski, 2003; Czaplewski and Morgan, 2012; Morgan et al., 2019; this paper; Table 5): the two emballonurids; an extinct genus and species of Mormoopidae, *Koopmanycteris palaeomormoop*s; and an extinct genus and species of basal noctilionoid in the extinct family Speonycteridae, *Speonycteris aurantiadens*. I-75 has two additional taxa with Neotropical affinities not found in Brooksville 2, *Speonycteris naturalis* and an indeterminate genus of Natalidae, and Brooksville 2 has an indeterminate genus of Molossidae not found in I-75. The mormoopid and natalid from I-75 are the oldest known members of those two families and the two species of *Oligopteryx* from this site are the oldest emballonurids from the New World. A single upper molar of a vespertilionid from I-75 represents the only bat from this site or Brooksville 2 that does not have clear Neotropical affinities. Another new genus and species of emballonurid, *Karstopteryx gunnelli*, occurs in the latest Oligocene (~24 Ma) Buda LF in Florida. The early Miocene (~18 Ma) Thomas Farm LF adds four species with Neotropical affinities (Czaplewski et al., 2003a; Morgan and Czaplewski, 2003; this paper): the diclidurine emballonurid *Floridopteryx poyeri*, described here; the extinct genus and species of natalid *Primonatalus prattae*; and two molossids near *Tadarida* or *Mormopterus*. *Floridopteryx* is the earliest diclidurine and *Primonatalus prattae* is the oldest named natalid. The early Miocene Miller LF from Florida has an unidentified molossid that may be similar to one of the two molossids from the slightly younger Thomas Farm LF (Morgan and Czaplewski, 2012). As discussed in more detail above under Paleoecology, the occurrence of a diverse fauna of bats with tropical affinities corroborates a tropical or subtropical climate in peninsular Florida during the Oligocene and early Miocene. The disappearance of Neotropical bats from Florida after the early Miocene suggests a change to a more temperate climate as indicated by the presence of a middle Miocene paleoflora in the Florida panhandle with warm temperate affinities (Jarzen et al., 2010; Lott et al., 2019). The rarity of bats with tropical affinities from North American Tertiary sites outside of Florida probably reflects the more temperate climate in western North America after the Eocene (Czaplewski et al., 2008; Morgan and Czaplewski, 2012).

Excluding a rather diverse fauna of vespertilionids from Oligocene, Miocene, and Pliocene sites from Florida and the western US of presumed temperate affinities, only about half a dozen other Tertiary records of bats with Neotropical affinities are known from North America (Czaplewski et al., 2008, 2018; Morgan et al., 2013). The oldest is the molossid *Wallia scalopidens* from the middle Eocene (late Uintan) Swift Current Creek LF in Saskatchewan, Canada (Storer, 1984; Legendre, 1985), but also see Smith et al. (2012) who questioned the molossid affinities of *Wallia*. A somewhat older record, from the middle Eocene (Bridgerian NALMA) Tabernacle Butte LF in Wyoming (McKenna et al., 1962), has been questionably allied with the Molossidae (Legendre, 1985). Two new genera and three new species of early middle Eocene (Bridgerian) bats were recently described from the Elderberry Canyon LF in Nevada (Czaplewski et al., 2022). Among these three species, *Volactrix simmonsae* and *Palaeochiropteryx sambuceus* belong to extinct, archaic bat families and *Sonor handae* appears to be an early member of the Vespertilionidae. None of these new middle Eocene species has obvious Neotropical affinities. An undescribed genus and species of phyllostomine phyllostomid from the early Miocene Lirio Norte and Centenario local faunas in Panama is one of the earliest known members of the Phyllostomidae and the only Tertiary bat reported from Central America (Morgan et al., 2013). Three other North American records of bats with Neotropical affinities are post-Interchange molossids (Table 5; Czaplewski, 1993; Czaplewski et al., 2003a, 2018): *Eumops* cf. *perotis* from McRae Wash, Arizona and *Tadarida* sp. from Deer Park, Kansas are both late Pliocene (early Blancan NALMA) in age, whereas a record of *Tadarida* sp. from Macasphalt Shell Pit, Florida is early Pleistocene (late Blancan).

Two bats from late Pliocene and early Pleistocene Interchange sites in North America appear to be of South American origin and were probably participants in the Plio-Pleistocene phase of the GABI, the large extant molossid *Eumops* cf. *perotis* from the late Pliocene McRae Wash LF in Arizona (Czaplewski, 1993) and the extinct desmodontine vampire bat *Desmodus archaeodaptes* (Phyllostomidae) from three early Pleistocene sites in Florida (Morgan et al., 1988). *Eumops* sp. is first known from the middle Miocene La Venta Fauna in Colombia (Czaplewski, 1997; Czaplewski et al., 2003b). The genus *Desmodus* is now known from five sites that date to the late Pliocene/early Pleistocene phase of the GABI, a large species, *Desmodus* sp., similar to the extinct *D. draculae*, from Uruguay and Venezuela (Ubilla et al., 2019; Czaplewski and Rincon, 2020) and a smaller extinct species, *D. archaeodaptes*, from the early Pleistocene (~1-2 Ma) Inglis 1A, Haile 16A, and Haile 21A LFs (type locality) in Florida (Morgan et al., 1988). It seems most likely that vampire bats evolved in South America and followed their favored prey/blood donor species (large xenarthans?) northward into North America during the Interchange (Morgan et al., 1988; Morgan, 1991). Two Neotropical chiropteran families, Mormoopidae and Natalidae, are present in several Oligocene and/or early Miocene faunas in Florida but are unknown in South America before the late Pleistocene. Mormoopids and natalids apparently evolved in North America in the Oligocene if not earlier, and were also participants in the GABI, dispersing southward across the Panamanian isthmus to South America sometime after the early Pliocene (Morgan and Czaplewski, 2003; Morgan et al., 2019).

Previous hypotheses on the origins and evolutionary histories of the various families of Neotropical bats were based primarily on the geographic distribution of the modern chiropteran fauna (Koopman, 1970, 1976, 1982), and more recently including phylogenetic relationships based on molecular genetics, with minimal input from the fossil record (Teeling et al., 2005; Lim, 2009, 2010). These hypotheses suggested that members of the six endemic Neotropical families, including five families in the superfamily Noctilionoidea (Furipteridae, Mormoopidae, Noctilionidae, Phyllostomidae, Thyropteridae) and the Natalidae, as well as two pantropical families (Emballonuridae, Molossidae), either evolved in South America or reached South America early in their evolutionary history (Oligocene or Miocene), and then dispersed northward overwater to the West Indies or Central America before the Pliocene, or overland to Central America following the connection of the two continents at the Panamanian isthmus in the early Pliocene (O'Dea et al., 2016). Prior to their arrival in South America, an African or Gondwanan origin has been hypothesized for seven of these bat families (Teeling et al., 2005; Lim, 2009), including Emballonuridae, the five families in the Noctilionoidea and Molossidae. Among the nine families of bats found in South America, only the New World representatives of the Vespertilionidae were considered to have a North American origin. Discoveries of large samples of fossil bats from the Oligocene and early Miocene of Florida over the past three decades establish that more than half of the New World families with tropical affinities now have a Tertiary fossil record in North America (Czaplewski et al., 2003a; Morgan and Czaplewski, 2003, 2012; Czaplewski and Morgan, 2012; Morgan et al., 2013, 2019; this paper), complicating the evolutionary history and biogeography of these groups. With the earliest Western Hemisphere records for the Emballonuridae, Mormoopidae, and Natalidae, as well as the extinct basal noctilionoid family Speonycteridae, from the early Oligocene of Florida, a South American or African/Gondwanan origin for the New World members of these groups is in question.

The Oligocene to Pliocene fossil record of the Chiroptera from the Western Hemisphere now consists of 11 genera and 17 species from South America and 22 genera and 28 species from North America (Czaplewski, 2005; Czaplewski et al., 2008; Morgan and Czaplewski, 2012; Antoine et al., 2016; Ubilla et al., 2019; Czaplewski and Rincon, 2020; this paper). The numbers of genera in these two faunas, particularly North America, are comparable to the generic diversity of Oligocene, Miocene, and Pliocene chiropteran faunas from Africa and Australia, and are considerably more diverse than the post-EoceneTertiary bat fauna from Asia (Gunnell and Simmons, 2005). The North American post-Eocene Tertiary bat fauna consists of 10 genera and 14 species belonging to 5 families now primarily tropical in their distribution, mostly from the Oligocene and early Miocene of Florida (Table 5), as well as 12 genera and 15 species of Vespertilionidae from Florida and western North America that lack obvious Neotropical affinities (Czaplewski et al., 2008; Morgan and Czaplewski, 2012; Morgan et al., 2019; this paper). The combined Tertiary New World chiropteran fauna with Neotropical affinities consists of 7 families, 18 genera, and 30 species (Table 5), compared to 2 families, 3 genera, and 3 species known prior to 1990, a nearly four-fold increase in families, six-fold increase in genera, and ten-fold increase in species. Only the molossid genus *Eumops* is known from the Tertiary of both continents, with a middle Miocene record from Colombia and a post-Interchange late Pliocene record from Arizona (Czaplewski, 1993, 1997; Czaplewski et al., 2003b).

The significant additions to the New World Tertiary chiropteran record over the past 30 years reflect a concerted effort by a large number of paleontologists to collect and screenwash sediments from fossil sites in both North America and South America, in particular from the middle Miocene of La Venta, Colombia (Czaplewski, 1997; Czaplewski et al., 2003b; and recent fieldwork by Nancy Simmons, Camilo López-Aguirre, and associates), the Eocene through late Miocene of the western Amazon Basin in Peru and Brazil (Czaplewski, 1996; Czaplewski and Campbell, 2004, 2017; Antoine et al., 2016), and Oligocene and early Miocene karst deposits in Florida (Pratt, 1989, 1990; Czaplewski and Morgan, 2000, 2012; Czaplewski et al., 2003a; Morgan and Czaplewski, 2003, 2012; Morgan et al., 2019; this paper). With a few notable exceptions, bats are generally rare in Tertiary fossil sites in the Western Hemisphere, primarily owing to the scarcity of pre-Pleistocene karst deposits in North America, outside of Florida, and the absence of Tertiary karst deposits in South America containing bats. In comparison, widespread karst and lacustrine deposits in Europe have produced the most diverse Tertiary chiropteran fauna known from any of the continents (Sigé and Legendre, 1983; Gunnell and Simmons, 2005). The ongoing efforts of paleontologists in North America and South America to screenwash Tertiary vertebrate fossil deposits will continue to improve the fossil record of the Chiroptera in the Western Hemisphere.

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We dedicate this paper to our good friend and colleague Dr. Gregg F. Gunnell, whose untimely passing in 2017 saddened all who knew him. We honor his memory with the description of a new genus and species of emballonurid bat, *Karstopteryx gunnelli*. Gregg was the Director of the Division of Fossil Primates at the Duke Lemur Center. He made numerous contributions to chiropteran paleontology, in particular from Africa, including late Eocene and early Oligocene bats from the Fayum Depression in Egypt, Pliocene bats from Kenya and Morocco, and early Pleistocene bats from Olduvai Gorge in Tanzania. We are especially grateful for his meticulous editing of our two chapters for the 2012 book on the Evolutionary History of Bats. We greatly miss Gregg's legendary knowledge of fossil mammals, and above all his friendship.

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APPENDIX 1. Modern comparative specimens of Emballonuridae and outgroups examined in this study. Species identification, museum acronym, catalog number, sex, basic locality information, and nature of specimen (e.g., cranium and mandible, skull and skeleton) are provided for each specimen. The taxonomy follows Simmons (2005).

Emballonuridae. New World. *Balantiopteryx io*: USNM 267343 (♂), Guatemala, Izabal, Bohos, skull and mandible. *Balantiopteryx plicata*: USNM 146943 (♂), Mexico, Baja California, Santa Anita, skull and mandible; USNM 559432 (♂), Mexico, Nayarit, San Blas, skull and mandible; OMNH 26646 (♂), Mexico: Colima: Colima: 1 km NE Cardona; OMNH 26681 (♀), Mexico: Colima: Manzanillo: Playa de Oro. *Centronycteris centralis*: USNM 503827 (♀), Panama, Canal Zone, Barro Colorado Island, skull and skeleton; USNM 535021 (♂), Panama, Canal Zone, Barro Colorado Island, skull and mandible. *Cormura brevirostris*, USNM 315139 (♂), Panama, Almirante, skull and mandible; USNM 464551 (♀), Panama, Bocas del Toro, Cayo Nancy, skull and mandible. *Cyttarops alecto*: USNM 566432 (♀), Costa Rica, Limon, Tortuguero, skull and skeleton. *Diclidurus albus*: USNM 407098 (♂), Venezuela, Amazonas, San Juan, skull and mandible; USNM 418688 (♂), Venezuela, Zulia, El Rosari, skull and mandible; OMNH 26706 (♂), Mexico: Colima: Manzanillo: Playa de Oro. *Diclidurus ingens*: USNM 407091 (♀), Venezuela, Amazonas, San Juan, skull and mandible. *Diclidurus isabellus*: USNM 388542 (♂), Venezuela, Amazonas, Boca Mavaca, skull and mandibls; USNM 388548 (♀), Venezuela, Amazonas, 68 km SE of Esmeralda, skull and mandible. *Peropteryx macrotis*: UF-M 6935 (sex unknown), Guatemala, Petén, Tikal, skull and skeleton; USNM 313146 (♂), Panama, Buena Vista, skull and mandible; USNM 393000 (♂), Brazil, Para, Belem, Mocambo, skull and mandible. *Peropteryx kappleri*: USNM 418630 (♀), Venezuela, Falcon, Cerro Caridad, skull and mandible; USNM 461844 (♀), Colombia, Valle, SW of Jamundi, skull and mandible. *Peropteryx trinitatis*: USNM 338936 (♂), Guyana, Rupununi, Dananawa, skull and mandible. *Rhynchonycteris naso*: USNM 315101 (♂), Panama, Almirante, skull and mandible; USNM 562211 (♀), Peru, Madre de Dios, skull and skeleton. *Saccopteryx bilineata*: UF 6971-M (♀), Guatemala, Petén, Tikal, skull and skeleton; USNM 549311 (♀), Brazil, Para Altamira, skull and skeleton; OMNH 14334 (♀), Mexico: Colima: Cuauhtémoc: El Cobano; *Saccopteryx canescens*: USNM 392996 (♂), Brazil, Para, Belem, Mocambo, skull and mandible. *Saccopteryx gymnura*: USNM 460080 (♀), Brazil, Para, Belem, Mocambo, skull and mandible. *Saccopteryx leptura*: USNM 392999 (♂), Brazil, Para, Belem, Mocambo, skull and skeleton; USNM 513430 (♂), Ecuador, Zamora-Chinchipe, Los Encuentros, skull and mandible.

Old World. *Coleura afra*: USNM 350817 (♂), Kenya, Diana, skull and mandible; USNM 350831 (♂), Kenya, Diana, skull and skeleton. *Emballonura alecto*: USNM 458529 (♂), Philippines, Leyte, Inopacan, skull and mandible; USNM 458549, (♂), Philippines, Leyte, Inopacan, skull and mandible. *Mosia nigrescens*: USNM 277114 (♀), Papua New Guinea, Emirau Island, skull and mandible. *Saccolaimus flaviventris*: USNM 284163 (♂), Australia, Northern Territory, Port Langde, skull and mandible. *Saccolaimus peli*: USNM 481709 (♀), Liberia, Grand Gedeh, Tars Town, skull and mandible. *Saccolaimus pluto*: USNM 458550 (♂), Philippines, Negros, Dumaguete, skull and mandible. *Saccolaimus saccolaimus*: USNM 294813 (♀), Thailand, Ratchaburi, Tapa, skull and mandible. *Taphozous melanopogon*: USNM 251744 (♀), Thailand, Bangkok, skull and mandible; USNM 252225 (♂), Thailand, Bangkok, skull and mandible. *Taphozous melanopogon*: USNM 458557 (♀), Philippines, Maripipi Island, Maripipi, skull and skeleton. *Taphozous nudiventris*: USNM 300209 (♂), Egypt, Saqqara, skull and mandible.

Non-Emballonuridae examined. Nycteridae. *Nycteris grandis*: USNM 411849, Ghana, Volta, Kpeve. *Nycteris hispida*: AMNH 184478, Sudan, Bahr el Ghazal, Yirol Dist. *Nycteris thebaica*: AMNH 168140, Botswana, Ngamiland, Mohembo. Rhinopomatidae. *Rhinopoma microphyllum*: AMNH 244388, Pakistan.

APPENDIX 2. Selected characters and character states of the upper and lower dentition and dentary of Emballonuridae. Characters 1-65 are from Ravel et al. (2016), translated from French; characters 66-85 are new to this study. The numbered characters (1-85) and character states within each character (i.e., 0, 1, 2) listed below are analyzed in Table 4 for 14 species of extinct and extant species of Emballonuridae, including three extinct species from Florida described in this paper. The dental terminology used in the characters below, in Table 4, and in the text follows Czaplewski et al. (2008) and differs somewhat from that used by Ravel et al. (2016). Equivalent dental terms are both used in this appendix. Our term is listed first followed by the Ravel et al. (2016) term in parentheses (e.g., labial = buccal; anterior = mesial; posterior = distal; paracingulum= precingulum; metacingulum = postcingulum, etc.).

CHARACTERS FROM RAVEL ET AL. (2016)

Dentary

1. Coronoid process height
0. high (about twice the height of the dental row)
1. low

2. Coronoid process apex
0. sharp
1. rounded

3. Horizontal ramus
0. gracile (lower than height of molars)
1. robust (greater than height of molars)

4. Coronoid process angle
0. vertical (almost perpendicular to horizontal ramus)
1. oriented posteriorly

Lower dentition

5. Number of lower incisors
0. three incisors on each mandible
1. two incisors on each mandible

6. Number of lower premolars
0. three premolars on each mandible
1. two premolars on each mandible

7. Lower incisors lobes
0. bilobed
1. trilobed

8. Lower incisors relative size
0. incisors of equivalent size

APPENDIX 2. Cont.

8. Lower incisors relative size (cont.)
1. i3 widest of lower incisors
2. i1 widest of lower incisors

9. c1 labial (=buccal) cingulum
0. strong (well developed and continuous)
1. weak (very thin or absent)

10. c1 root
0. straight
1. curved posteriorly

11. c1 posterior basin
0. extended posteriorly
1. reduced

12. p2 size
0. reduced
1. not reduced (size equivalent to p4)
2. larger than p4

13. p3 roots
0. one root
1. two roots

14. p3 crown
0. well developed
1. very small

15. p4 size
0. well developed (size larger than the anterior premolar, with a protoconid and talonid)
1. reduced (size smaller than the previous premolar

16. p4 talonid
0. extended posteriorly
1. reduced
2. absent

17. p4 paraconid
0. present
1. absent

APPENDIX 2. Cont.

18. p4 metaconid
0. present
1. absent

19. Lower molar trigonid cusps
0. high and well separated
1. low

20. m1 trigonid
0. lingually open
1. compressed anteroposterioly (=mesiodistally)

21. m2 trigonid
0. lingually open
1. compressed anteroposterioly (=mesiodistally)

22. m1: distance between the paraconid and metaconid
0. less than distance between metaconid and entoconid
1. greater than or equal to distance between metaconid and entoconid

23. m2: distance between the paraconid and the metaconid
0. less than distance between metaconid and entoconid
1. greater than or equal to distance between metaconid and entoconid

24. m3: distance between the paraconid and the metaconid
0. less than distance between metaconid and entoconid
1. greater than or equal to distance between metaconid and entoconid

25. m1-m2 trigonid width
0. less than that of talonid
1. greater to that of talonid
2. equivalent to width of talonid

26. m1-m2 entoconid
0. high and inclined posteriorly (similar in size to metaconid)
1. absent or very reduced
2. moderate and upright (smaller than metaconid)

27. m1-2 entocristid
0. straight
1. slightly curved
2. strongly curved/sharply V-shaped

APPENDIX 2. Cont.

28. m1-m2 cristid obliqua meets postcristid
0. medial; meets posterior wall of trigonid (= protocristid) at junction between metacristid and postprotocristid (dental terminology of Ravel et al., 2016).
1. lingual; meets posterior wall of trigonid (= protocristid) in more lingual position than junction between metacristid and postprotocristid.
2. labial; meets posterior wall of trigonid (= protocristid) in more labial position than junction between metacristid and postprotocristid

29. m1-m2 hypoconulid position
0. central and posterior position on postcristid between entoconid and hypoconid
1. on postcristid slightly more labial than the entoconid
2. very close and posterior to entoconid

30. m1-m2 postcristid
0. straight
1. curved posteriorly

31. m3 talonid width
0. equivalent to width of trigonid
1. less than the width of trigonid

32. m3 hypoconulid
0. present
1. weak/absent

Upper dentition

33. C1 labial (=buccal) cingulum
0. present
1. absent
2. very thin and discontinuous

34. C1 lingual cingulum
0. strongly curved
1. almost straight

35. C1 posterior break in cingulum
0. present
1. absent

36. Number of upper premolars
0. three
1. two
2. one

APPENDIX 2. Cont.

37. P4 talon basin
0. elongated or expanded lingually
1. compressed labiolingually (=buccolingually)

38. P4 crown, anterolabial (=buccomesial) lobe
0. with pronounced anterolabial (=buccomesial) lobe
1. without anterolabial (=buccomesial) lobe
2. with weak anterolabial (=buccomesial) lobe

39. P4 anterolingual (=mesiolingual) tubercle/root
0. present
1. absent

40. M1-M2 ectoflexus
0. double
1. simple and anterior to mesostyle
2. simple and central

41. M1-M2 “V” of ectoloph asymmetry
0. weak
1. pronounced

42. M1 inclination of labial (=buccal) margin
0. strong
1. weak

43. M1-M2 position of mesostyle
0. lingual, set back from labial (=buccal) margin
1. labial, extends outward from labial (=buccal) margin

44. M1-M2 labial (=buccal) cingulum
0. discontinuous along labial (=buccal) border
1. continuous along labial (=buccal) border

45. M1-M2 labial (=buccal) cingulum at mesostyle
0. present
1. absent

46. M1 parastyle
0. connected to the preparacrista
1. isolated from preparacrista
2. absent

APPENDIX 2. Cont.

47. M1-M2 paraloph
0. present
1. absent

48. M1-M2 metaloph
0. present
1. absent

49. M1-M2 paracingulum (=precingulum)
0. wide
1. very thin to absent

50. M1-M2 metacingulum (=postcingulum)
0. wide
1. thin

51. M1-M2 protocone
0. well developed; larger than metacone and paracone
1. reduced; equal to or smaller than metacone and paracone

52. M1-M2 connection of posterior extension of postprotocrista
0. connects with metacingulum (=postcingulum)
1. connects with lingual cingulum
2. does not connect with any other structure
3. connects with hypocone

53. M1-M2 connection of preprotocrista
0. connects to paracingulum (=precingulum)
1. meets base of paracone

54. M1-M2 protofossa extension
0. extends along anteroposterior (=mesiodistal) axis
1. short

55. M1-M2 posterior (=distal) opening of protofossa
0. closed posteriorly (distally) by postprotocrista
1. open

56. M1-M2 level of protofossa
0. low and opening onto talon basin
1. high and without a connection with talon basin

APPENDIX 2. Cont.

57. M1-M2 hypocone
0. present and well developed
1. present but small/low
2. absent

58. M1-M2 posterior (=distal) flattening of talon
0. strong
1. weak
2. absent

59. M1-M2 posterior (=distal) border of talon
0. rounded
1. with posterolingual (=distolingual) lobe or extension

60. M1-M2 orientation of talon
0. posterior (=distal)
1. posterolingual (=distolingual)

61. M1-M2 lingual (=buccal) cingulum
0. thick
1. thin/absent

62. M3 size
0. more than half the width of M2
1. less than half the width M2

63. M3 metacone
0. small
1. well developed (equivalent to paracone)
2. absent

64. M3 lingual (=buccal) cingulum
0. present
1. absent

65. M3 premetacrista
0. present
1. absent

NEW CHARACTERS FROM THIS STUDY

66. c1 lingual cingulum
0. well developed
1. thin or absent

APPENDIX 2. Cont.

67. c1 anterolingual cusp
0. present
1. absent

68. c1 posterolingual cusp
0. present
1. absent

69. p2 occlusal shape
0. rounded
1. elongated anteroposteriorly

70. p4 occlusal shape
0. rounded
1. elongated anteroposteriorly

71. m1 and m2 morphology
0. similar, both with lingually open trigonids
1. similar, both with lingually compressed trigonids
2. different, m1 with open trigonid, m2 with more compressed trigonid

72. m1 trigonid
0. open lingually
1. compressed

73. m1/m2 protoconid and metaconid placement
0. protoconid anterior to metaconid
1. metaconid anterior to protoconid
2. protoconid and metaconid at same level

74. m1/m2 protocristid
0. transverse or horizontal to toothrow
1. posterolingually inclined from protoconid to metaconid
2. anterolingually inclined from protoconid to metaconid

75. m1/m2 entoconid
0. smaller than metaconid
1. equal in size to metaconid
2. larger than metaconid

76. m1/m2 hypoconulid
0. well developed
1. present but small

APPENDIX 2. Cont.

77. m1/m2 hypoconid and entoconid placement
0. hypoconid anterior to entoconid
1. entoconid anterior to hypoconid
2. hypoconid and entoconid at same level

78. m1/m2 postcristid
0. transverse or horizontal to toothrow
1. posterolingually inclined from hypoconid to entoconid
2. anterolingually inclined from hypoconid to entoconid

79. m1/m2 labial cingulum
0. thick/strong
1. thin, continuous
2. thin, discontinuous

80. m3 talonid
0. very narrow, less than half the width of trigonid
1. narrow, about half the width of trigonid
2. broad, greater than half to almost equal to width of trigonid

81. m3 entoconid
0. well developed, about equal to metaconid
1. small to absent, much smaller than metaconid

82. C1 anterolingual cusp
0. present
1. absent

83. C1 posterolingual cusp
0. present
1. absent

84. M1 parastylar region, including parastyle and parafossa
0. weakly reduced, parastyle connected to ectoflexus
1. reduced, parastyle isolated
2. reduced, parastyle absent

85. M1 preparacrista
0. weakly reduced, ~½ the length of M2 preparacrista
1. short, less than ½ the length of M2 preparacrista
2. absent