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Molossid bats from the late Tertiary of Florida with a review of the Tertiary Molossidae of North America

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The fossil history of molossids in the North American Tertiary is among the poorest for any family of bats. The oldest definite record is of *Wallia scalopidens* of middle Eocene (Uintan) age from Saskatchewan, Canada. One of the youngest records is of *Eumops* cf. *E. perotis* from the late Pliocene (late early Blancan) of Arizona, USA. New occurrences detailed herein from the middle and late Tertiary of Florida, USA, begin to fill in the 40-million-year gap between the previous records. They are: (1) an abraded upper molar of an indeterminate genus from the Brooksville 2 locality, Hernando County, of late Oligocene (Arikareean) age; (2) a large and a small upper molar pertaining to two congeneric species similar to *Tadarida* and *Mormopterus*, from the Thomas Farm local fauna, Gilchrist County, of early Miocene (early Hemingfordian) age; and (3) a distal humerus from a *Tadarida* of an unknown species that is larger than extant *Tadarida brasiliensis* and similarly sized but differently proportioned than in the extinct Pleistocene species *Tadarida constantinei*. The last specimen is from the Macasphalt Shell Pit, Sarasota County, and is of late Pliocene (late Blancan) age.

Key words: Chiroptera, Molossidae, Florida, Oligocene, Miocene, Pliocene, *Tadarida*, *Mormopterus*

Introduction

The Tertiary history of the chiropteran family Molossidae in North America is among the weakest for any bat family on the continent. Only five localities have produced putative free-tailed bats amounting to eight total specimens, most of which are isolated teeth. The present paper slightly improves that record, adding three more teeth and revisiting a humerus fragment that was previously reported (Morgan, 1991). The scarcity of molossid fossils in North America contrasts with that in the European Tertiary, where the family is relatively well represented (Legendre, 1984a, 1984c; Storch, 1999).

The oldest North American record of a possible molossid is a fragmentary mandible with an m2 of early middle Eocene age (late Bridgerian land mammal age) from Tabernacle Butte, Sublette County, Wyoming. This specimen, first reported by McKenna *et al*. (1962), originally was thought to represent a bat of an undescribed genus and species, but at the time the family to which it belonged could not be determined and it was not named. Although we have not examined this specimen, the m2 was said by McKenna *et al*. (1962) to lack a hypoconulid. This is unlike the condition in most microchiropteran bats, in which the lower molars (at least m1 and m2) usually have an obvious hypoconulid. However, Legendre

(1985) later tentatively identified this same jaw fragment as '?Molossidae.' If the specimen is indeed a molossid, then it would be the oldest member of the family.

The oldest definite molossid in North America is *Wallia scalopidens*, from the middle Eocene (late Uintan land mammal age) of Swift Current Creek, Saskatchewan, Canada (Storer, 1984). This taxon was originally placed in Proscalopidae (Insectivora) by Storer (1984), but Legendre (1985) placed *Wallia* in the Molossidae and agreed with Storer that a lower jaw originally referred to *Wallia* does not belong to a bat. The type specimen of *Wallia scalopidens* is a right M1; of the original hypodigm, three additional upper teeth do represent bats and are probably referable to *Wallia*.

Following these early records, there is a huge gap in the North American history of the Molossidae until the late Tertiary, during which only three other instances have been recorded in the Pliocene. One of these is of an isolated lower molar purportedly representing a 'bat, near *Tadarida*' in the Blanco local fauna of Crosby County, northern Texas (Dalquest, 1975). Dalquest (1975) suggested that the tooth resembled the m2 of the extant species *Tadarida brasiliensis*. However, we borrowed and re-examined this specimen (Texas Tech University Museum No. TTU-P 6135) and found that it does belong to a bat, but not a molossid. Although its entoconid is damaged, this molar is clearly myotodont, whereas most molossids including *Tadarida* and *Nyctinomops* have nyctalodont lower molars (Menu and Sigé, 1971; Legendre, 1984*a*, 1984*b*, 1985). Instead, the specimen from the Blanco local fauna probably pertains to a vespertilionid but is indeterminate. A definite Pliocene molossid is represented by a single tooth, an upper third molar identified as *Eumops* cf. *E. perotis* from the late Pliocene (late early Blancan land mammal age) McRae Wash fauna of the San Pedro

Valley, Arizona (Czaplewski, 1993). Finally, Morgan (1991) reported the distal portion of a humerus of *Tadarida* from the late Pliocene (late Blancan) Macasphalt Shell Pit fauna of Florida; this specimen is discussed in more detail below.

In Florida, many vertebrate fossil-bearing localities are associated with paleokarst features (Hulbert, 2001) and many of these have produced small to large numbers of fossil bats. There are three localities from which four Tertiary specimens of molossids have been recovered in Florida. From oldest to youngest, these are Brooksville 2, Hernando County (late Oligocene); Thomas Farm, Gilchrist County (early Miocene); and Macasphalt Shell Pit, Sarasota County (late Pliocene). Although these records are scrappy, they begin to fill the gap in the middle Tertiary history of the family in North America.

MATERIALS AND METHODS

In the descriptions of teeth that follow, we use the terminology of Legendre (1984*c*). Upper teeth are designated by upper case letters (e.g., P4 for upper fourth premolar) and lower teeth are designated by lower case letters (e.g., m1 for lower first molar). For the humerus we follow the terminology used by Czaplewski and Morgan (2000). The Florida molossid fossils described here are from the vertebrate paleontology collection of the Florida Museum of Natural History, University of Florida, Gainesville (UF). Ages are given in Ma (mega-annum or millions of years before present) and ka (kilo-annum or thousands of years before present). Measurements were made with an optical reticle on an Olympus SZX9 stereomicroscope calibrated with a stage micrometer. All measurements of fossils are in mm.

Description of Localities

Brooksville 2 locality — This site is in an abandoned limestone quarry about 10 km northeast of Brooksville, Hernando County, in central Florida (Fig. 1). Vertebrate fossils were found in clay and sand fillings in karstic solution features within the marine, early Oligocene Suwannee Limestone. The mammalian fauna indicates a 'medial' or late early
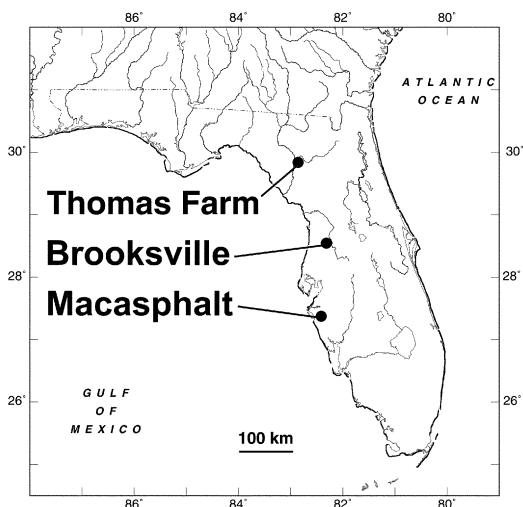
FIG. 1. Map of Florida showing fossil localities mentioned in the text: Thomas Farm (Hemingfordian); Brooksville 2 (Arikareean); Macasphalt Shell Pit (Blancan)

Arikareean land mammal age, between 25 and 28 Ma (Hayes, 2000). According to the subdivisions of the Arikareean proposed by Woodburne and Swisher (1995), the Brooksville 2 fauna represents the Ar2, which is late Oligocene in age (Tedford *et al*., 1996; MacFadden and Hunt, 1998). The Brooksville 2 local fauna includes at least 46 species of vertebrates composed of fish, amphibians, reptiles, a bird, and 27 species of mammals (Hayes, 2000). Among the mammals are bats of the families Mormoopidae (1 undescribed species), ?Phyllostomidae (1 undescribed species), Emballonuridae (2 undescribed species), Vespertilionidae (1 species), and Molossidae (1 species) (authors' unpubl. data). The remainder of the chiropteran fauna from Brooksville 2 is currently under study. The most abundant remains of Chiroptera represent the mormoopid and emballonurids; the molossid is represented by a single worn tooth.

Thomas Farm locality — This site, located 12 km north of Bell in Gilchrist County in northern peninsular Florida, has produced one of the most diverse early Miocene land vertebrate faunas in eastern North America. The fossiliferous sediments at Thomas Farm consist of alternating layers of clay and sand almost completely filling a 30 m deep sinkhole/cave complex developed in Eocene marine limestone (White, 1942; Auffenberg, 1963; Pratt, 1989, 1990). Faunal lists and bibliographies were published by Ray (1957); Olsen (1962); and Webb (1981). Previous studies of the mammalian fauna from Thomas Farm (briefly summarized in Czaplewski

and Morgan, 2000, and Morgan and Czaplewski, in press) indicate a late early Hemingfordian land mammal age (early Miocene; between 18 and 19 Ma). The Thomas Farm local fauna is composed of approximately 90 species of vertebrates, including nearly 70 species of small vertebrates and 23 species of large mammals (see Webb, 1981 for the most current faunal list). Among the small mammals are at least nine species of bats, including one species each in the Neotropical families Emballonuridae and Natalidae, five species in the family Vespertilionidae, and two species of Molossidae (Lawrence, 1943; Czaplewski and Morgan, 2000; Morgan and Czaplewski, In press). Lawrence (1943) described the first bats from Thomas Farm, the vespertilionids *Miomyotis floridanus* and *Suaptenos whitei*, and Czaplewski and Morgan (2000) described the large vespertilionid *Karstala silva*. The earliest known natalid, *Primonatalus prattae,* was recently described from Thomas Farm (Morgan and Czaplewski, In press; we do not consider *Honrovits* [Beard *et al*., 1992] to be a natalid; see Czaplewski *et al*., In press). Thomas Farm has the largest known sample of bats from any pre-Pleistocene fossil deposit in North America. Over 75% of the chiropteran sample consists of vespertilionids, whereas fossil elements of the molossids are the rarest in the deposit, with only two teeth found to date.

Macasphalt Shell Pit locality — This site, in an abandoned commercial shell mine about 8 km east of Sarasota, Sarasota County, in southwestern Florida, has yielded one of the most diverse vertebrate faunas of Pliocene age in Florida. The vertebrate fossils were mixed with marine, estuarine, freshwater, and terrestrial molluscs in a dark, organic, sandy layer within the shallow marine shell beds of the Pinecrest Sand Member of the Tamiami Formation (Petuch, 1982; Jones *et al*., 1991). In addition to the molluscs, the fauna includes numerous fish, amphibians, reptiles, 46 species of birds, and 23 species of mammals (Morgan and Ridgway, 1987; Jones *et al*., 1991; Emslie, 1992, 1998). The Macasphalt Shell Pit paleofauna represents the late Blancan land mammal age (late Pliocene, 2.2–2.7 Ma). Four genera of mammals from Macasphalt, including the armadillos *Dasypus* and *Holmesina*, the ground sloth *Glossotherium*, and the capybara *Neochoerus* (Morgan and Ridgway, 1987; Jones *et al*., 1991), are taxa of South American origin that participated in the Great American Biotic Interchange (Stehli and Webb, 1985) by crossing the Isthmus of Panama soon after it became dry land. The association of these South American immigrants with the three-toed horse *Nannippus* constrains the age of the Macasphalt fauna to a restricted time interval in the late Pliocene after the onset of the Interchange at

about 2.7 and before the extinction of *Nannippus* at about 2.2 Ma. Petuch (1982) interpreted the predominantly aquatic fauna of the Macasphalt Shell Pit as indicating a quiet, shallow-water, estuarine depositional environment near a river. Only one bat fossil is known from this locality, a humerus fragment of *Tadarida* sp., which was interpreted as one of the early South American immigrants entering North America as a part of the Interchange (Morgan, 1991).

SYSTEMATIC PALEONTOLOGY

Order Chiroptera
Family Molossidae

Genus indeterminate

A single upper molar (M1; UF 182897; Fig. 2A) of a molossid was recovered among the mammalian fossils from Brooksville 2. Preservation of the tooth is unusual; the specimen is bright red brown and highly polished so that the formerly sharp crests are rounded and many details of enamel morphology are obliterated and unclear. Presumably this condition is due to abrasion by water-borne sediments; many bones from Brooksville 2 show evidence of fluvial transport. Notably, the skeletal elements belonging to bats other than the molossid are some of the best preserved specimens in the Brooksville fauna. Although they are isolated teeth and fragments of jaws and limb bones, they are not waterworn. This suggests that the other kinds of bats might have roosted in the karst system near where their bones were found, but that the molossid perhaps roosted, died, or its bony remains were initially deposited farther away and later transported to the site where they were found as fossils.

Measurements of the tooth are: labial anteroposterior length (parastyle to metastyle), 2.00 mm; transverse width, 2.75 mm. The specimen is about the same size as the M1 in the living species *Nyctinomops macrotis*. The molar generally resembles that of most molossids in having a relatively large talon that is crowned with a conical hypocone. A tiny ridge runs from the hypocone to the posterior wall of the protocone but does not reach the postprotocrista. There is a strong paraloph that connects with a small paraconule on the preprotocrista. The metaloph is absent. There seems to have been a small gap between the postprotocrista and the metacingulum, but this is not certain because of abrasion. The preprotocrista was probably originally continuous through the paracingulum to the parastyle, but now is interrupted near the anterior base of the paracone. There is no lingual cingulum around the protocone or talon. In occlusal view, the labial edge of the tooth is nearly straight from metastyle to parastyle, although this condition may be due to the styles being worn away.

Compared to other Tertiary molossids in which the upper molars are known, the Brooksville M1 differs from the M1 of *Wallia* in being much larger, having a much narrower paracingulum, lacking a metaloph, lacking an indentation of the stylar shelf between the mesostyle and parastyle, and lacking a lingual cingulum. It differs from *Mormopterus faustoi* in larger size, in having the postprotocrista not distinctly continuous with the metacingulum, and in lacking an indentation in the stylar shelf between the parastyle and mesostyle. It differs from *Mormopterus colombiensis* in much larger size, having a much smaller talon, weaker paraloph and no metaloph, and lacking deep indentations between the three labial styles. It differs from most *Eumops* species in lacking a lingual cingulum and an indentation between parastyle and mesostyle. It also differs from some species of *Eumops* in lacking indentation between the mesostyle and metastyle. It differs from *Potamops* in much smaller size, in having a stronger talon with distinct hypocone, and lacking an indentation between mesostyle and parastyle. It differs from *Tadarida thersites* in lacking notches between labial styles, in
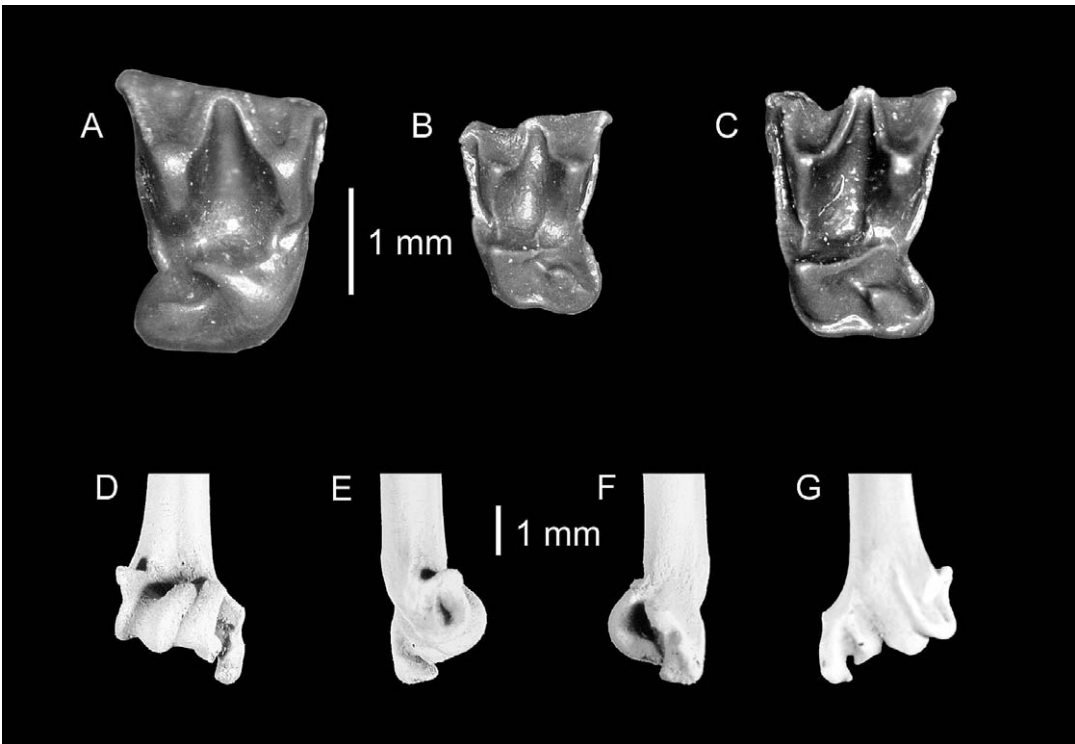
FIG. 2. Fossils of Molossidae from the late Tertiary of Florida. A–C, occlusal views of upper molars. (A) Molossidae, genus indet., UF 182897, right M1 from Brooksville 2. (B) *Tadarida* or *Mormopterus*, UF 108662, left M1 from Thomas Farm. (C) *Tadarida* or *Mormopterus*, UF 108663, left M2 from Thomas Farm. D–G, *Tadarida* sp., UF 209993, distal half of right humerus from Macasphalt Shell Pit. Dark original specimen was coated with ammonium chloride powder for photography: (D) anterior view, (E) lateral view, (F) medial view, and (G) posterior view

having the anterolingual base of the protocone situated farther posteriorly, and in lacking the distinct indentation between the base of the protocone and the base of the hypocone or talon. In the fossil, the post-protocrista is completely separated from the hypocone; whereas, in *T. thersites,* the hypocone and its anterior crest are merged into the postprotocrista. It differs from *Tadarida* (*Mops*) *rusingae* in being much smaller with much less robust crests. The fossil differs from *Nyctinomops* in lacking a metaloph and lingual cingulum. The Brooksville M1 is much larger than Species A and larger than Species B from Thomas Farm (see below), and further differs from both of these in lacking a metaloph, lingual cingulum, and talon cingulum, in having a narrower paracingulum, in having a (probably) more weakly crested hypocone, and in lacking an indentation between the parastyle and mesostyle. The Brooksville specimen probably represents a new taxon of Molossidae, but the single available tooth is too small a sample to name and is also less than ideal for a diagnosis because of the abrasion it suffered.

Tadarida or *Mormopterus* species A

Of the two specimens of molossids recovered from Thomas Farm, UF 108662 is a virtually unworn left M1 (Fig. 2B). Measurements are: labial anteroposterior length (parastyle to metastyle), 1.45 mm;

transverse width, 1.95 mm. This specimen is approximately the same size as the M1 in *Tadarida brasiliensis*. The tooth has a relatively long and strong paraloph and metaloph. The metaloph extends from the base of the metacone to the postprotocrista. The postprotocrista bypasses the hypocone. The talon is rounded and supports a prominent hypocone that has small pre- and post-hypoconal crests. The lingual cingulum is absent at the base of the protocone, weak anterior to the protocone, and strong between the protocone and hypocone. There is also a strong cingulum on the posterior side of the talon. The postprotocrista and talon cingulum do not quite connect with the lingual end of the metacingulum. The preprotocrista extends from the protocone to the parastyle as a paracingulum. The paraloph does not connect with the preprotocrista. There is a normal W-shaped ectoloph in which the first commissure (preparacrista) is shorter than the others. In occlusal view, there is a shallow indentation along the labial edge of the tooth between the parastyle and mesostyle, but no indentation between mesostyle and metastyle. Furthermore, there are no labial cingula.

The fossil consistently differs from the M1 in *Cheiromeles*, *Myopterus*, *Molossus*, *Eumops*, *Promops*, and *Molossops* in having a paraloph and metaloph, and from *Neoplatymops* in having a paraloph; it also differs from these genera in other details that vary from genus to genus but these details need not be individually listed here. In *Tomopeas* the paraloph and metaloph are present, but the Florida fossil differs from *Tomopeas* in having a more prominent parastyle and lingual cingulum, and in having a postprotocrista that bypasses the hypocone.

Compared with extant members of the Tadaridinae, the Florida fossil differs from *Otomops* in having a strong talon and distinct hypocone separated from the postprotocrista; from *Mops* in having a paraloph and metaloph; from *Mormopterus* (*Sauromys*) in having a broader, less laterally-compressed talon; from *M.* (*Platymops*) in lacking a short curved labial cingulum and indentation anterior to the metastyle and in having a rounded rather than angular occlusal outline of the talon; and from *Mormopterus kalinowskii* and *M. phrudus* in having a lingual cingulum. The fossil also differs from *Nyctinomops* in having a shorter paraloph and metaloph that do not unite and extend to the protocone, in lacking a labial indentation in the occlusal outline posterior to the mesostyle, and in lacking a small stylar cuspule and associated labial cingulum between the cuspule and the metastyle. It differs from the M1 of *T. brasiliensis* in having a shorter, single metaloph that is close to the anterior base of the metacone instead of extending along the anterior wall of the metacone well into the trigon basin (protofossa) or being double (i.e., with two metalophs, a short one at the base of the metacone and a longer one along the anterior wall of the metacone; this feature is variable among individuals). The Florida specimen differs from other extant species of *Tadarida* (*teniotis*, *lobata*) in possessing a metaloph. It is shorter relative to the transverse width of *Tadarida thersites*; moreover, the fossil differs from *T. thersites* in having a paraloph and metaloph, in lacking indentation between the mesostyle and metastyle, and in not bulging anteriorly on the anterior margin of the tooth.

By comparison with other fossil molossids in which the upper molars are known, this Thomas Farm specimen has a more distinct lingual cingulum and talon cingulum, and a narrower paracingulum than in *Wallia scalopidens*; it also has different proportions, being shorter anteroposteriorly and wider transversely than *Wallia*. It has a relatively much larger talon and hypocone than *Mormopterus faustoi* and *M. colombiensis*. It is much smaller than

Potamops mascahehenes and has a distinct hypocone.

In summary, the smaller of the two Thomas Farm molossid teeth most closely resembles tadaridines, especially *Tadarida* (including *Rhizomops*) and some species of *Mormopterus*, yet differs in various details from all molossids. It might represent a new taxon; however, given the largely undocumented inter- and intraspecific variation in details of dental morphology, we feel it is prudent not to base a new taxon on the tooth at this time.

Tadarida or *Mormopterus* species B

The second molossid specimen from Thomas Farm, UF 108663, a left M2 (Fig. 2C), closely resembles Species A described above and is possibly congeneric with it. Species B is larger than Species A and matches it in morphological details except in having a metaloph that does not reach the postprotocrista, a postprotocrista that is continuous with the metacingulum, a lingual cingulum that is stronger and continuous around the base of the protocone and talon, and a weaker post-hypoconal crista. There are also no hints of labial cingula.

Measurements are: labial anteroposterior length (parastyle to metastyle), 1.80 mm; transverse width, 2.35 mm. The specimen is about 19% longer and 17% wider than Thomas Farm Species A. It is about the same size or slightly larger than the M2 in *Nyctinomops aurispinosus* and in *N. femorosaccus*.

Most of the differences between Species A and other molossids also separate Species B from them. As in Species A above, Species B most closely resembles *Mormopterus*, *Nyctinomops*, and *Tadarida* (*Rhizomops*). Species B differs from *Mormopterus* in having a strong lingual cingulum and talon cingulum, and in having no labial indentation between mesostyle and metastyle. It differs from *Nyctinomops* in having

a much shorter paraloph and metaloph, and in having no labial cingulum extending anteriorly from the metastyle halfway toward the mesostyle. It differs from *T.* (*Rhizomops*) *brasiliensis* in having a weaker metaloph that barely bends forward along the anterior wall of the metacone into the trigon basin, in having a lingual cingulum that is continuous around the base of the protocone, and in lacking an indentation in the labial margin between mesostyle and metastyle. In the fossil, the anterior edge (in occlusal view) does not strongly bulge forward as in *T. thersites*. The hypocone of the fossil is distinct and separate from the postprotocrista; whereas, in *T. thersites*, it is merged into the postprotocrista. Furthermore, the fossil is unlike *T. thersites* in having a better defined lingual cingulum, in having a metaloph, in having a slightly stronger (yet still weak) paraloph, and in having a weaker labial indentation between the mesostyle and the metastyle.

Tadarida sp.

A long bone fragment of a molossid from Macasphalt Shell Pit is the only chiropteran fossil yet known from the site. The specimen is UF 209993, the distal half of a right humerus (Fig. 2D–G). It is recognizable as the humerus of a molossid in having a straight shaft, a relatively narrow distal articular surface that is in line with the long axis of the shaft, a long and curved spinous process of the epitrochlea, a medial ridge of the capitulum that is inclined at a strong angle to the long axis of the bone, and no olecranon fossa.

The fossil humerus is much larger than humeri of *Tomopeas ravus* and much smaller than humeri of *Eumops glaucinus, E. underwoodi, E. perotis,* and *N. macrotis*. It is approximately the size of *N. aurispinosus*. Compared to the observed range of measurements of this bone in *Tadarida*

TABLE 1. Measurements (in mm) of the distal humerus of molossids including a Florida Pliocene fossil from Macasphalt Shell Pit (UF 209993), a sample of the extinct species *Tadarida constantinei* from the Pleistocene of New Mexico, and modern specimens of selected species. Measurements are given as mean (where sufficient numbers of specimens were available) and observed range (in parentheses). The 'spinous process' is measured as the length of the distal spinous process projecting beyond the distal edge of the trochlea

Character	*Tadarida* sp. (UF 209993)	*T. brasiliensis*	*T. constantinei*	*Nyctinomops femorosaccus*	*N. macrotis*	*N. aurispinosus*
Greatest distal width	2.95	2.54 (2.34–2.75)	3.18 (2.96–3.33)	2.73 (2.70–2.75)	3.27 (3.25–3.30)	2.85
Width of distal articular surface	2.50	2.20 (2.05–2.30)	2.64 (2.50–2.71)	2.30 (2.25–2.35)	2.80 (2.70–2.90)	2.45
Diameter of shaft	1.40	1.25 (1.13–1.32)	1.41 (1.29–1.50)	1.30 (1.30)	1.65 (1.65)	1.45
Length of spinous process	0.55	0.54 (0.50–0.60)	0.44 (0.42–0.50)	0.45 (0.45)	0.63 (0.60–0.65)	0.55
Proximo-distal diameter of lateral ridge of capitulum	1.75	1.57 (1.40–1.70)	1.86 (1.71–2.08)	1.48 (1.45–1.50)	1.82 (1.80–1.85)	1.70
Sample size	1	20	10	2	2	1

constantinei (Table 1), the Macasphalt humerus is differently proportioned; it is smaller in greatest distal width, at the low end of the observed range in width of distal articular surface and diameter of lateral ridge of capitulum, yet it is equal in the mean diameter of the shaft and has a longer spinous process. Compared to the range of measurements in *T. brasiliensis*, the Macasphalt humerus is greater in all measurements except in the length of the spinous process, in which it is about equal to the average.

UF 209993 differs in shape from the humerus of *Molossus* in having a small notch separating the spinous process from the medial side of the trochlea rather than being fused to it; in having a shorter, less curved, and blunt rather than pointed spinous process; and in having a more strongly angled medial ridge of the capitulum. It differs from the distal humerus of *Eumops perotis* in having a less curved and blunt rather than pointed spinous process, and in having a much more strongly angled medial ridge of the capitulum. It differs from the humerus of *E. underwoodi* in having a more strongly angled medial ridge of the capitulum and a much smaller tubercle on the epitrochlea for the tendon of origin of the pronator teres muscle. It differs from the humerus of *Nyctinomops* (*macrotis, femorosaccus, aurispinosus*), *Mormopterus* ([*Platymops*] *setiger*), and *Otomops* (*martiensseni*) in having a more strongly angled medial ridge of the capitulum, the grooves in the distal articular surface are deeper, and the small tubercle on the proximal-lateral side of the lateral ridge of the capitulum is more prominent and extends further proximally. The Macasphalt humerus shows no differences in details of shape from the humeri of *T. brasiliensis* and *T. constantinei*, and also resembles the illustration of a distal humerus of *T. stehlini* provided by Legendre and Sigé (1983).

DISCUSSION

Among the known extant and extinct molossids, the Tertiary molossids from Florida most closely resemble *Tadarida*. The two isolated molars from Thomas Farm also share many similarities with *Mormopterus*. It is not possible to distinguish between these two genera based on the currently available fossil teeth. The distal humerus from the late Pliocene Macasphalt Shell Pit represents a *Tadarida* larger than *T. brasiliensis*, and is about the same size as the humerus of the extinct Pleistocene species *T. constantinei* (Table 1) from Slaughter Canyon Cave (= New Cave) in New Mexico (Lawrence, 1960). The precise age of the *Tadarida* from Slaughter Canyon Cave is unknown, although unsuccessful attempts to radiocarbon date the guano deposits in which the bat fossils occur suggest this site is older than 40 ka. Fossils that may be referable to *T. constantinei* are also known from two other Pleistocene cave deposits, Mammoth Cave in Kentucky (Jegla and Hall, 1962) and Hamilton Cave in West Virginia (Repenning and Grady, 1988; Winkler and Grady, 1990). Microtine rodents from Hamilton Cave (Repenning and Grady, 1988; Winkler and Grady, 1990) indicate a late early Pleistocene age (medial Irvingtonian land mammal age, about 0.8 –0.9 Ma). The sediments from Mammoth Cave containing the *Tadarida* fossils were dated at greater than 38 ka (Jegla and Hall, 1962), and more recent study of the Mammoth Cave fauna suggests that it may also be Irvingtonian (R. Toomey, pers. comm.). Although a large species of *Tadarida* possibly referable to *T. constantinei* is known from several Irvingtonian sites, we do not refer the Macasphalt humerus to that species because of the paucity of Blancan material available, several proportional differences noted above, and the disparity in age.

The Molossidae occur worldwide in tropical regions, with a few species found in temperate latitudes on each of the continents (Hill and Smith, 1984; Koopman, 1993). The Neotropical region in Middle and South America supports a diverse fauna of molossids, including seven species (*Eumops glaucinus*, *E. perotis*, *E. underwoodi*, *Molossus molossus*, *Nyctinomops femorosaccus*, *N. macrotis*, and *Tadarida brasiliensis*) that extend their ranges northward into the Nearctic region in northern Mexico and/or the southern United States (Koopman, 1993). Cenozoic fossils representing the Molossidae are best known from Europe (Legendre, 1985), whereas smaller samples of Tertiary molossids are known from North America (reviewed herein), South America (Czaplewski, 1997; see below); Africa (Arroyo-Cabrales *et al*., 2002), Asia (Legendre *et al*., 1988; Mein and Ginsburg, 1997), and Australia (Hand, 1990; Hand *et al*., 1997, 1999). Legendre (1984*a*, 1984*c*, 1985) reviewed the systematics and historical biogeography of Cenozoic Molossidae, including the sparse Tertiary record of this family in North America and South America. Subsequent publications (Morgan, 1991; Czaplewski, 1993, 1997), along with the Florida fossils reported herein, allow us to update the Tertiary history of the New World Molossidae.

The oldest record of the Molossidae is from the early middle Eocene (late Bridgerian) Tabernacle Butte fauna of Wyoming (McKenna, 1962), although the identification of this fragmentary dentary as a molossid was considered tentative (Legendre, 1985). The next oldest molossid is also from North America, *Wallia scalopidens* from the middle Eocene (late Uintan) of Swift Current Creek, Saskatchewan, Canada (Storer, 1984). The Swift Current Creek fauna is 42–44 Ma in age (Storer, 1984), whereas the earliest molossid from the Old World, *Cuviermops* from the late Eocene of

France, is slightly younger, about 39 Ma in age (Legendre, 1985). Florida fossils from the late Oligocene (early Arikareean) Brooksville 2 fauna and the early Miocene (early Hemingfordian) Thomas Farm fauna are the first known mid Cenozoic molossids from North America. The Florida Oligocene and Miocene molossids, consisting of three isolated teeth, cannot be identified to genus pending recovery of additional material. An isolated upper tooth of *Eumops* cf. *E. perotis* from the late Pliocene (late early Blancan) McRae Wash fauna of Arizona (Czaplewski, 1993) and a distal humerus of *Tadarida* from the late Pliocene (late Blancan) Macasphalt Shell Pit fauna in Florida (Morgan, 1991) complete the sample of North American pre-Pleistocene molossids.

The Tertiary record of molossids in South America is presently as meager as that from North America, although several of the South American fossils are considerably more complete than any molossid fossils known from North America. There are three known genera and three named species of Tertiary molossids from South America. *Mormopterus faustoi* was described on the basis of a partial skeleton from the Oligocene (Deseadan land mammal age) of the Tremembé-Taubaté Basin, São Paulo state, Brazil (Paula Couto, 1956, 1983). A tooth of *Eumops*, seven isolated teeth described as the new species *Mormopterus colombiensis*, and a skull fragment with P4-M3 described as the new genus and species *Potamops mascahehenes* are known from the middle Miocene La Venta fauna (Laventan land mammal age) of Colombia (Czaplewski, 1997). An unidentified molossid rather similar to *Neoplatymops* is also recorded in the late Miocene of Peru (Czaplewski, 1996).

The Molossidae are one of only three or four families of bats so far known to be shared by North America and South America before the Great American Biotic Interchange, the others being Emballonuridae, Vespertilionidae, and possibly Phyllostomidae (Czaplewski, 1997; Morgan and Czaplewski, 2002; authors' unpubl. data). Despite their ability to fly, bats rarely cross wide oceanic water barriers and as such most bats probably did not cross the Bolivar Trough separating North and South America prior to the connection of these continents at the Panamanian Isthmus in the Pliocene. Bats have only rarely been included in discussions of the Interchange but there is some evidence that one genus of molossid, *Eumops*, may have evolved in South America and immigrated to North America in the Pliocene as a member of the Interchange fauna. Czaplewski (1997) identified *Eumops* in the middle Miocene La Venta fauna in Colombia, whereas this genus is unknown in pre-Interchange sites in North America with the oldest record being a tooth of *Eumops* cf. *E. perotis* from the late Pliocene of Arizona (Czaplewski, 1993). *Eumops perotis* is a living species found in the southwestern United States, northern Mexico, and South America, but is absent from much of tropical Middle America. There are no other fossil records of *Eumops* in North America prior to the late Pleistocene (Morgan, 1991; Czaplewski, 1993). Most species of *Eumops* currently have a Neotropical distribution in Middle and South America, with only three species, *E. glaucinus*, *E. perotis*, and *E. underwoodi*, extending their ranges northward into the southernmost United States (Koopman, 1993). It seems likely based on current evidence that *Eumops* evolved in South America and then immigrated northward into North America with the remainder of the Interchange fauna in the Pliocene.

The origin of *Tadarida* in the Western Hemisphere is more problematic. The oldest specimen in the New World that can be confidently referred to *Tadarida* is the distal humerus from the late Pliocene Macasphalt

site in Florida. On the basis of that record, Morgan (1991) hypothesized that *Tadarida* may have had a Neotropical (South American) origin in the New World, and then immigrated to North America in the late Pliocene during the Interchange. The subsequent discovery of teeth similar to *Tadarida* and *Mormopterus* from the Miocene of Florida and the absence of a pre-late Pleistocene fossil record of *Tadarida* from South America suggest another hypothesis is possible. The presence of *Tadarida*-like teeth in the early Miocene of Florida and definite fossils of *Tadarida* from the late Pliocene of Florida and the early to medial Pleistocene of Kentucky, New Mexico, and West Virginia, suggest that the New World representatives of this genus may have originated in North America. *Tadarida, Mormopterus,* or a closely related genus may have immigrated to North America from Eurasia across the Bering land bridge in the early Miocene or before. Several species of *Tadarida* and *Mormopterus* are known from Oligocene and Miocene sites in Europe and Asia (Legendre, 1985; Legendre *et al.*, 1988; Mein and Ginsburg, 1997), including fossils referred to *Rhizomops*, the genus (according to Legendre, 1984*a*), or more likely subgenus, that includes *T. brasiliensis* and presumably *T. constantinei*. Although *Mormopterus* is known in the Oligocene and Miocene of South America (and unknown in North America), the only South American fossil record of *Tadarida* consists of specimens of *T. brasiliensis* from a late Pleistocene cave deposit in Brazil (Czaplewski and Cartelle, 1998). An alternative biogeographic history to that proposed by Morgan (1991) would be that *Tadarida* immigrated from Eurasia to North America in the Miocene, and then immigrated to South America in the late Pliocene after the onset of the Interchange. The chiropteran fossil record from South America is particularly poor between the late Miocene and the late Pleistocene; therefore, future fossil discoveries may well alter this biogeographic scenario. With respect to the ultimate origins of molossids in South America, it is possible that molossids and other bat families could have initially entered South America in the Eocene-Oligocene from Africa, as phylogenetic evidence suggests for primates and caviomorph rodents (Flynn and Wyss, 1998), but their ancestry and derivation are unknown because there is no phylogenetic, morphological or paleontological evidence from South America or Africa to support or refute such a claim.

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