Gary S. Morgan and Nicholas J. Czaplewski. The North American fossil record of bats (Mammalia: Chiroptera) from cave and karst deposits. *Journal of Cave and Karst Studies*, v. 87, no. 4, p. 265-313. DOI:10.4311/2024PA0116

THE NORTH AMERICAN FOSSIL RECORD OF BATS (MAMMALIA: CHIROPTERA) FROM CAVE AND KARST DEPOSITS

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Abstract

Bats are the group of mammals most closely associated with caves. More than half of the 45 living species of bats from temperate North America (NA) are cave-dwellers in the families Vespertilionidae, Molossidae, Phyllostomidae, and Mormoopidae. Bats that inhabit caves also die in caves, leaving their skeletons to become preserved in fossil deposits on the cave floor. During the latter half of the Pleistocene epoch (~10 ka to 1 Ma), bats have an excellent fossil record in NA caves, primarily vespertilionids of extant species. We recognize only two extinct species of vespertilionids, *Myotis rectidentis* (late Pleistocene) and *Corynorhinus alleganiensis* (middle Pleistocene). Two other extinct bats are known from late Pleistocene cave deposits in the US: a large vampire, *Desmodus stocki* (Phyllostomidae), in 8 caves in the southern US, 4 in Mexico, and 6 karst deposits in Florida, and the extinct mustached bat, *Pteronotus pristinus* (Mormoopidae) of Cuba, but is also known from a karst deposit in Florida. The record of bats from late Pleistocene cave deposits in Mesoamerica consists of 11 caves in Mexico and 1 in Belize. The only other extinct Pleistocene bat in Mesoamerica besides *Desmodus stocki* is the giant vampire, *D. draculae*, known from Loltún Cave in Mexico and Cebada Cave in Belize. A diverse fauna of Quaternary bats is known from several hundred cave deposits across the West Indies, including more extinct species (eight) than are found in Pleistocene deposits in continental NA: six extinct species from Cuba, *Pteronotus pristinus* and *Mormoops magna* (Mormoopidae; also known from Hispaniola) and *Artibeus anthonyi*, *Cubanycteris silvai*, *Phyllops silvai,* and *Phyllops vetus* (Phyllostomidae); *Tonatia saurophila* (Phyllostomidae) known only from Jamaica; and *Phyllonycteris major* (Phyllostomidae) from Puerto Rico, Antigua, and Marie Galante. There are also 18 living species of bats that underwent local extinction on one or more Antillean islands during the Holocene, including the extant vampire bat *Desmodus rotundus* in Cuba.

The oldest NA cave deposits containing fossil bats are early Pleistocene in age (~0.8–1.0 Ma) in West Virginia, Texas, Colorado, and New Mexico. NA bat fossil sites older than early Pleistocene are primarily paleokarst deposits (sinkholes, fissures, solution cavities) in peninsular Florida. The richest of these are: Inglis 1A (early Pleistocene, ~2 Ma), with 7 species, including the oldest NA record of *Desmodus* and the only eastern NA record of *Antrozous*; Thomas Farm (early Miocene,~18 Ma), a sediment-filled sinkhole/cave complex containing 9 species including *Primonatalus prattae*, the oldest named species in the strictly cave-dwelling family Natalidae, *Floridopteryx poyeri* in the Emballonuridae; and 3 extinct genera of vespertilionids, *Karstala*, *Miomyotis*, and *Suaptenos*; and two Oligocene (26–30 Ma) fissure fills, I-75 and Brooksville 2, with 7 species of bats, including *Koopmanycteris palaeomormoops*, the oldest member of Mormoopidae; 2 species of *Speonycteris* representing an extinct family (Speonycteridae) with Neotropical affinities; and *Oligopteryx floridanus* and *O. hamaxitos*, the earliest New World emballonurids. Although karstic deposits are widely distributed in NA, they mostly lack fossil bats, except in Florida. We suspect undiscovered Tertiary karst deposits with bats exist elsewhere in NA.

INTRODUCTION

Caves are well known as producers of vertebrate fossils around the world and through a substantial span of Earth history (Andrews, 1990; Simms, 1994; Harris, 2005; Lundelius, 2006), especially in the Quaternary (Jass and George, 2010; Schubert and Mead, 2012). We review the fossil record of bats (Mammalia: Chiroptera) in North America (NA) from caves and other karst deposits, from the early Oligocene (~30 million years ago [Ma])] through the end of the Pleistocene (~10 thousand years ago [ka]). Our review covers the entire North American continent from Alaska and Canada south to Panama and also includes the extensive fossil record of bats from caves in the West Indies. We focus mostly on the continental United States (US) because the record is more complete, including several hundred caves that have produced Pleistocene vertebrate faunas, many of which contain fossil bats (Martin, 1972; Kurtén and Anderson, 1980; Harris, 1985, 2023; FAUNMAP, 1994; Czaplewski et al., 2008). We note that Hawaii also has an important record of fossil bats from lava tube caves (Ziegler et al., 2016). However, Hawaii is considered part of Oceania so its fossil bat record is not discussed here. During the latter half of the Pleistocene (between about 10 ka and 1 Ma), bats have an excellent fossil record in NA caves, primarily insectivorous species in the family Vespertilionidae. We discuss several late Pleistocene cave deposits that have produced large samples of bats, including caves in Arizona, New Mexico,

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and Oklahoma. The record of fossil bats from Mesoamerica consists of about a dozen late Pleistocene cave deposits in Mexico and one in Belize. The West Indies has a rich Late Quaternary (late Pleistocene and Holocene) chiropteran record from caves (Morgan, 2001), including underwater caves with large fossil bat samples from Abaco in the Bahamas and the Dominican Republic (Steadman et al., 2007; Velazco et al., 2013; Soto-Centeno and Steadman, 2015). We are not aware of vertebrate fossils from caves in NA that are older than about 1 Ma. Older caves do exist, including several in Carlsbad Caverns National Park that are Miocene in age (~6–12 Ma) based on $^{40}Ar/^{39}Ar$ dates on sulfate minerals in cave deposits (Polyak et al., 1998), but these older caves do not contain fossil vertebrates. Older deposits containing abundant samples of bats, ranging in age from early Pleistocene to late Oligocene (~2 to 30 Ma), are known from Florida, but these are derived from karst features such as sinkholes, fissures, and solution cavities and not caves. In general, bats are more common and skeletally more complete as fossils in caves than in open sites, including fluvial, lacustrine, alluvial, and nearshore marine deposits (Kowalski, 1995; Eiting and Gunnell, 2009; Brown et al., 2019). However, the remarkable complete skeletons of bats in Eocene lake deposits from Messel in Germany and the Green River Formation in Wyoming are obvious exceptions (Smith et al., 2012; Rietbergen et al., 2023).

Figure 1A shows major regions of karst in the continental U. S. (Weary and Doctor, 2014). Many of these regions have caves containing Pleistocene deposits with bats and other vertebrates (Kurtén and Anderson, 1980; Harris, 1985), including (from east to west): Cenozoic marine limestones from Florida; Paleozoic carbonates in the Appalachian Mountains in Pennsylvania, Maryland, West Virginia, Virginia, Tennessee, Georgia, and Alabama; Paleozoic carbonates in western Kentucky, western Tennessee, and the Ozark Mountains in Missouri, Arkansas, and Oklahoma; Cretaceous limestones on the Edwards Plateau in Texas; and Paleozoic and Mesozoic carbonates in the Mountain West, including New Mexico, Arizona, Colorado, Utah, Nevada, and Wyoming. These are not the only areas in the continental US that have produced Pleistocene cave deposits with bats, with caves occurring in most states, including not only typical caves formed in carbonate rocks, but also caves formed as lava tubes or natural traps in areas with extensive volcanic deposits. An unusual type of karst occurs in the Southern Great Plains where the only modern caves are ephemeral, fast-eroding gypsum caves developed as salt-dissolution features in evaporite karst in Permian sandstone and siltstone formations (see Fig. 1; Johnson, 1989, 1996; Johnson and Neal, 2003). These gypsum caves in the Southern Great Plains have not yet produced Pleistocene vertebrate faunas.

Figure 1B indicates the distribution of carbonate rocks in NA, including not only the contiguous US but also Alaska, Canada, Mexico, Central America, and the West Indies (from a map of the global distribution of carbonate rocks; Ford and White, 2007; Hollingsworth et al., 2008). This map shows the widespread distribution of carbonate rocks in eastern and southern Mexico, in particular the Yucatán Peninsula, which also includes Belize and part of Guatemala, as well as more limited areas in Honduras, Nicaragua, and Costa Rica. Among the areas in Mesoamerica with extensive outcrops of carbonate rocks, the Sierra Madre Oriental in eastern Mexico and the Yucatán Peninsula in Mexico and Belize contain caves that have produced samples of fossil bats (Arroyo-Cabrales and Polaco, 2003; Czaplewski et al., 2003). This map also shows the four major islands in the Greater Antilles—Cuba, Hispaniola, Jamaica, and Puerto Rico—all of which have numerous carbonate caves containing fossil bats (Morgan, 2001; Dávalos and Turvey, 2012).

METHODS

We provide definitions of several terms we use in this paper (e.g., cave, karst, paleokarst) that may differ from the more traditional usage of these terms by cavers, cave geologists, and others. Our primary interest in this paper is how caves and karst features serve as natural cavities for the accumulation of vertebrate fossils, specifically bats. Online definitions (e.g., britannica.com; wikipedia.org) describe a cave as being a natural void in the ground that is large enough for a human to enter and usually extends to total darkness, to differentiate caves from rock shelters that are shallow and exposed to natural light and from fissures that are generally too small to allow human entry. This definition is especially important in Florida where caves containing vertebrate fossils are fairly uncommon, but karst-derived sinkholes, fissures, and solution cavities containing vertebrate fossils are commonplace. Caves normally form as underground voids by the dissolution of carbonate rocks through the action of weak carbonic acid and less commonly weak sulfuric acid. Less common types of caves include lava tubes formed in igneous rocks (e.g., basalt) and evaporite caves formed in gypsum. Karst is defined as a landform where the landscape is underlain by various types of carbonate rocks and is characterized by underground drainage and contains both caves and sinkholes and other karst-derived features (e.g., fissures, chimneys, solution cavities) that do not fit the definition of a cave. We also use the term paleokarst to refer to karst-derived features that formed in the geologic past.

We define several geographic regions here to eliminate any potential confusion regarding their usage. Our definition of North America (abbreviated throughout as NA) includes the entire North American continent, from Alaska and Canada south through the continental United States (US), Mexico, and Central America to Panama, including the West Indies. We recognize three major geographic subdivisions within North America: 1. Alaska, Canada, and the continental United States; 2. Mesoamerica (or Middle America), including Mexico and Central America; 3. West Indies. These

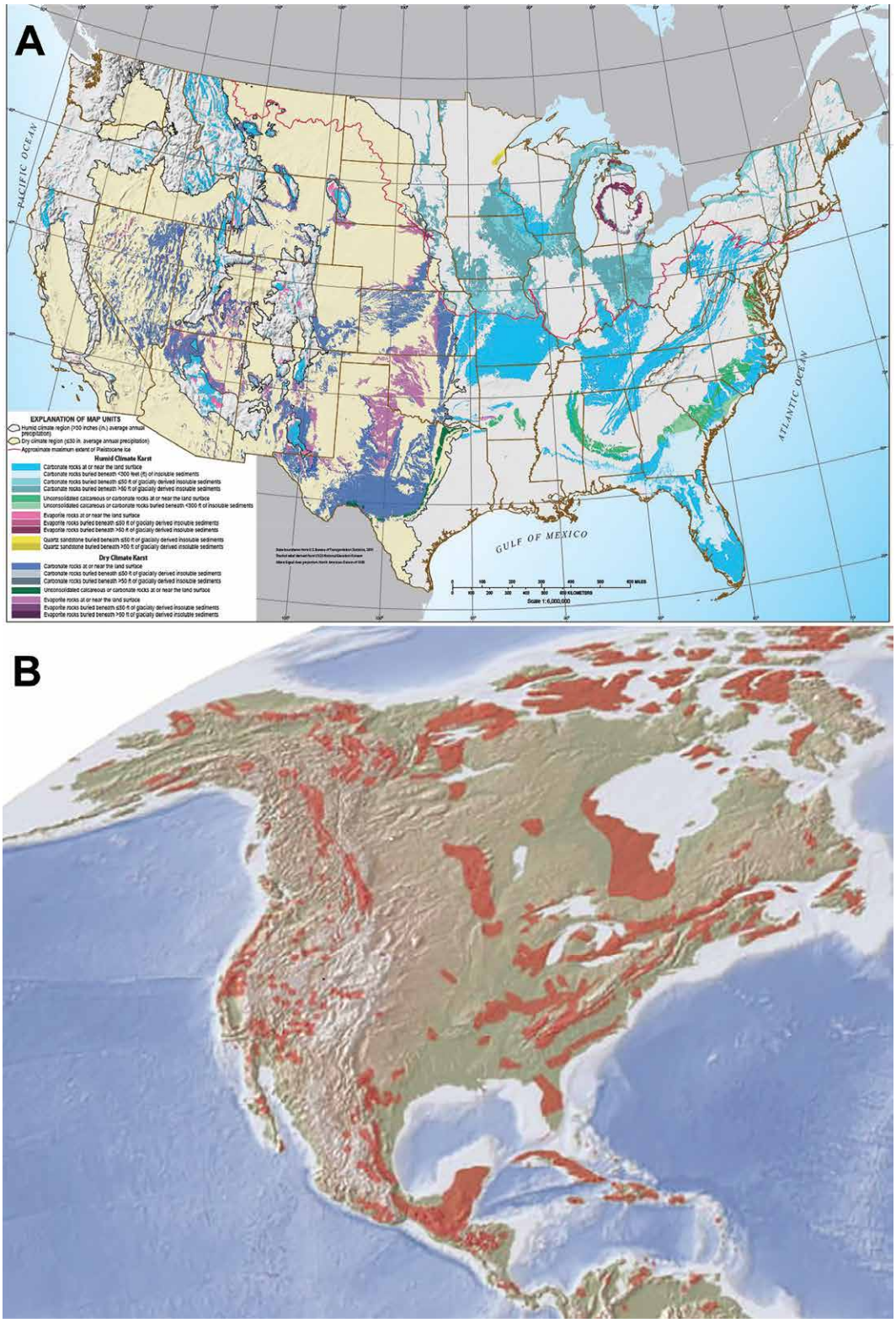

Figure 1. (A) Karst and potential karst areas in the contiguous United States (from Weary and Doctor, 2014). (B) North American distribution of carbonate rocks (from Ford and Williams. 2007; Hollingsworth et al., 2008).

three regions each have distinctive chiropteran faunas, with minimal overlap, and based on the fossil record, also had distinct bat faunas in the late Pleistocene. Within each of these three geographic regions, we discuss the occurrence of cave deposits containing fossil bats. We also recognize two biogeographic regions in NA, the Nearctic region and Neotropical region, with the boundary between these two regions located at approximately the Tropic of Cancer at 23° North latitude in central Mexico (Olson et al., 2001; Morrone, 2017; Morrone et al., 2022). The current Nearctic region is characterized by a boreal and temperate biota, occurring in the US, Canada, and northern Mexico. The current Neotropical region is characterized by a tropical biota and includes Mexico south of the Tropic of Cancer, Central America, the West Indies, and the tropical portion of South America (Morrone et al., 2022). The current bat fauna of Canada and the US consists primarily of insectivorous species in the family Vespertilionidae (33 species), most of which have temperate/Nearctic affinities. An additional 12 species in three other families, Phyllostomidae (4 species), Mormoopidae (1 species), and Molossidae (7 species), have primarily tropical/Neotropical affinities and occur at the northernmost limits of their geographic ranges in the southwestern US or Florida. Most of the 12 species with tropical affinities also occur in Mexico and farther south into Central America or the West Indies in the case of tropical species from Florida.

Figure 2. Bat fossils from late Pleistocene deposits in Three-Forks Cave in the Ozark Highland, Adair County, Oklahoma. (A) Finger is pointing to a cranium of the vespertilionid bat, *Myotis* sp., upside down and encrusted with flowstone. (B) A small jumble of bat wing bones in a muddy deposit on the floor of the cave.

Bats reach their greatest diversity or species richness in tropical regions (Hill and Smith, 1984; Nowak, 1994; Simmons, 2005), and this phenomenon is well illustrated in the transition from temperate/Nearctic to tropical/Neotropical bat faunas in the New World. A Neotropical chiropteran fauna characterizes central and southern Mexico (south of the Tropic of Cancer) and Central America, as well as the West Indies and the tropical regions of South America (López-Aguirre et al., 2018). The tropical bat fauna in Mesoamerica has a far larger number of species than does the bat fauna in temperate NA. For example, the modern chiropteran fauna of Mexico consists of about 140 species (Ceballos et al., 2014), and the bat fauna of northern Central America includes about 120 species (McCarthy et al., 1993), both of which are nearly three times the 45 species of mostly insectivorous bats that inhabit the US and Canada (Bradley et al., 2014). The Neotropical bat fauna also exhibits a much greater ecological diversity, with many species of fruit-eating and nectar-feeding bats (family Phyllostomidae, subfamilies Carolliinae, Glossophaginae, and Stenodermatinae), as well as bats that prey on other vertebrates (Phyllostomidae: Phyllostominae), including fish (Noctilionidae), and even feed on blood (Phyllostomidae: Desmodontinae). The Neotropical bat fauna occurs northward to the southern portion of the state of Tamaulipas along the Gulf of Mexico in northeastern Mexico, near the Tropic of Cancer (~23° N; Veracruzan province of Morrone et al., 2022), and extends somewhat farther north (~27° N) to the southern portion of the state of Sonora along the Gulf of California in northwestern Mexico (Pacific Lowlands province of Morrone et al., 2022). The West Indian islands have a very different bat fauna from the two other areas of NA, including many endemic genera and species, a result of their long isolation as oceanic islands (Baker and Genoways, 1978; Koopman, 1989; Morgan, 2001). The West Indian bat fauna is tropical in origin

and is considered a subset of the Neotropical region (Antillean subregion of Morrone et al., 2022), mostly composed of endemic genera or species in the families Phyllostomidae, Mormoopidae, and Natalidae, as well as several species in the Molossidae that include both endemic Antillean species and species that also occur in Mexico and Central America.

We used absolute dates to determine the age of some cave and karst faunas, including radiocarbon (^{14}C) dates for sites younger than 50 ka or other types of radioisotopic dates (U-series, $^{40}Ar/^{39}Ar$, etc.) for sites older than 50 ka. We also relied on mammalian biochronology using the North American Land Mammal Ages (NALMA) for continental faunas from NA (chapters in Woodburne, 2004): Prothero and Emry (2004) for the late Eocene and early Oligocene (Chadronian, Orellan, and Whitneyan NALMAs); Tedford et al. (2004) for the late Oligocene through earliest Pliocene (Arikareean, Hemingfordian, Barstovian, Clarendonian, and Hemphillian NALMAs), with updated ages for the Arikareean from Albright et al. (2008); and Bell et al. (2004) for the early Pliocene through late Pleistocene (Blancan, Irvingtonian, and Rancholabrean NALMAs). Although we do not discuss vertebrate faunas from continental NA that are younger than late Pleistocene, many fossil bat faunas from the West Indies are Holocene in age and are discussed here. Most radiocarbon-dated cave faunas from the West Indies are either late Pleistocene or Holocene in age. However, only a small percentage of Antillean cave faunas have been ^{14}C dated; and therefore, we cannot be certain of their exact age. In the case of undated West Indian faunas, we use the more inclusive, but less precise, term “Late Quaternary” that includes both late Pleistocene and Holocene faunas. The system of NALMAs does not apply to the West Indies because the Antillean land mammal fauna is highly endemic, sharing no non-volant species with the NA continent (Morgan and Woods, 1986; Dávalos and Turvey, 2012), and only about 10 species of bats that are of little use in biochronology. Minimal change in bat faunas occurred during the late Pleistocene and Holocene in continental NA, including only three extinct species and a few additional species that occurred outside their current geographic ranges (i.e., extralimital). The situation is quite different in the West Indies where numerous species of bats either became extinct or underwent extirpation or local extinction on certain islands during the Late Quaternary, occurring during the post-Columbian period after the arrival of Europeans about 500 years ago (Morgan, 2001; Soto-Centeno and Steadman, 2015).

BATS FROM PLEISTOCENE CAVE FAUNAS IN NORTH AMERICA, EXCLUSIVE OF FLORIDA

As noted in the Methods section, we divide North America into three regions, continental US, Alaska, and Canada (temperate NA), Mexico and Central America or Mesoamerica (tropical NA), and the West Indies, each of which has a distinctive modern and late Pleistocene bat fauna, with only minimal overlap with the other regions. The majority of fossiliferous cave deposits containing bats from the continental US, Alaska, Canada, and Mexico are late Pleistocene (Rancholabrean) in age (Kurtén and Anderson, 1980). West Indian caves produce bat faunas that are either late Pleistocene or Holocene in age (i.e., Late Quaternary). No cave deposits containing bats from Mesoamerica or the West Indies are known to be older than late Pleistocene (10-250 ka; Morgan, 2001; Arroyo-Cabrales and Polaco, 2003). A limited number of older cave faunas with fossil bats, dating to the late early and middle Pleistocene (Irvingtonian NALMA; ~0.25-1.0 Ma), are known from the US. No Pleistocene cave deposits in NA older than late early Irvingtonian (>~1 Ma) are known to contain bats or other vertebrates. However, karst deposits in Florida, dating from the late Pleistocene (~10 ka) to the early Oligocene (~30 Ma), are known to contain important samples of fossil bats (Morgan and Hulbert, 2008; Morgan and Czaplewski, 2012, 2023). The Florida fossil bat record is reviewed separately because the record is dominated by karst deposits and covers a much longer period of time.

Chiroptera from Late Pleistocene (Rancholabrean NALMA) Cave Deposits in the US and Canada

Cave fossil deposits containing bat fossils are known throughout the United States from sites dating to the late Pleistocene Rancholabrean NALMA (Kurtén and Anderson, 1980; Harris, 1985, 2023; FAUNMAP, 1994). Several reviews of Rancholabrean vertebrates from US states contain information on fossil bats, including Arizona (Mead et al., 2005) and New Mexico (Harris, 1993; Morgan and Harris, 2015). US cave sites of late Pleistocene age from which significant samples of fossil bats have been reported include: New Paris Number 4, Pennsylvania (Guilday et al., 1964); Clark’s Cave, Virginia (Guilday et al., 1977); Robinson Cave (Guilday, 1967; Guilday et al., 1969) and Lookout Mountain Cave (Gaudin et al., 2011), Tennessee; Mammoth Cave, Kentucky (Jegla and Hall, 1962; Widga and Colburn, 2018); Brynjulfson Caves, Missouri (Parmalee and Oesch, 1972); Three-Forks Cave, Oklahoma (Czaplewski et al., 2018); Inner Space Cavern (aka Laubach Cave) (Choate and Hall, 1967; Dorsey, 1977) and Hall’s Cave (Toomey, 1993; Moroz et al., 2021), Texas; Carlsbad Cavern and Muskox Cave, New Mexico (Baker, 1963; Logan, 1981; Kottkamp et al., 2022); and Arkenstone Cave and La Tetera Cave, Arizona (Czaplewski and Peachey, 2003; Czaplewski et al., this volume). The Appendix lists all species of bats known from late Pleistocene (Rancholabrean) cave deposits in the US and Canada, and the most important cave sites in which these species have been identified. However, this list is not comprehensive, as it does not include all late Pleistocene records of bats.

Harington (2011) reviewed the late Pleistocene vertebrate record from caves in Canada, documenting 22 cave sites from four Canadian provinces and the Yukon (Appendix). Eight species of bats in the Vespertilionidae are reported from Canadian Pleistocene cave deposits, and 12 of the 22 faunas have a least 1 species of bat (Harington, 2011). January

Cave in Alberta has the richest fossil bat fauna with 5 species, and 3 caves have 4 species each, Laflèche Cave and Mine Cave in Quebec and Elba Cave in Ontario. There are no extinct species of bats from Canadian Pleistocene caves, and all the identified species occur within their current geographic ranges. Jass et al (2022) suggested that the limited record of Pleistocene bats and other vertebrates from caves in Canada might be related to the presence of glacial ice, or possibly to effects of deglaciation. The Alaskan cave record for bats is extremely poor. In a review of the vertebrate fauna from 15 Pleistocene and Holocene cave sites from Prince of Wales Island and other smaller islands in the Alexander Archipelago in southeastern Alaska, Heaton and Grady (2003) reported one species of bat, *Myotis* sp., from several of the caves. Only five species of bats have been recorded from the modern fauna of Alaska, all vespertilionids.

Several factors are worthy of note with regard to the late Pleistocene chiropteran record of temperate North America. This record comprises almost entirely living species, mostly Vespertilionidae that still inhabit the general vicinity of the cave where the fossil remains were found. One of the few late Pleistocene records of a bat occurring outside its current range (i.e., extralimital) is a partial skull of the California leaf-nosed bat, *Macrotus californicus*, (Phyllostomidae) identified from a fissure deposit near Terlingua in southwestern Texas, about 450 km northeast of the closest living population in Chihuahua, Mexico, and about 800 km east of its current eastern limit in southeastern Arizona (Ray and Wilson, 1979). The few extralimital records of bats in NA late Pleistocene cave deposits is surprising, especially considering that extralimital records of various species of rodents and shrews, and the resulting "nonanalog" or "disharmonious" faunas, are characteristic of many of these same late Pleistocene cave faunas (Semken et al., 2010). This may be related to the relatively limited availability of caves for roosting habitat, the greater dependence of many bats on caves, or the differing distributional patterns of NA bats compared to other small mammals. No species of bats are endemic to Canada or Alaska, and the chiropteran fauna becomes limited in diversity in more northerly latitudes, consisting of just a few vespertilionids (Wilson and Ruff, 1999; Simmons, 2005). By comparison, there are numerous species of rodents and shrews now restricted to boreal habitats in Alaska and Canada that extended their ranges southward during glacial intervals, where they co-occurred in cave deposits in the central and southeastern US with other species of small mammals from more temperate habitats that still occur in the vicinity of the caves, creating nonanalog or disharmonious faunas (Semken et al., 2010).

Although upwards of 10 extinct species of bats have been described from late Pleistocene cave deposits in temperate NA (Kurtén and Anderson, 1980), we only recognize two of those species as valid, *Desmodus stocki* and *Myotis rectidentis*, and consider the latter species questionable and in need of further taxonomic study. Stock's vampire bat, *Desmodus stocki* (Phyllostomidae), is the most distinctive of these extinct species. This extinct vampire bat was originally described from San Josecito Cave in northern Mexico (Jones, 1958) and is also known from 18 other late Pleistocene sites in NA, including 3 other cave sites in Mexico (Arroyo-Cabrales and Polaco, 2003), 9 cave deposits in the US from California to West Virginia (Appendix; Ray et al., 1988; Czaplewski and Peachey, 2003; Grady et al., 2002; Czaplewski et al., this volume), and 6 karst deposits in Florida (Morgan, 1991). *D. stocki* is larger and differs in several cranial and postcranial characters from the living common vampire bat, *D. rotundus* (Morgan, 1991), that currently has a tropical distribution from Mexico south through Central America and much of South America (Koopman, 1988). The US sites containing *D. stocki* are all well north of the current geographic range of *D. rotundus*, suggesting the extinct species was able to tolerate cooler winter temperatures than the living species, whose northward distribution is limited by the 10°C winter isotherm in Mexico (McNab, 1973). There are no fossil records of *D. rotundus* north of its current geographic range in Mexico. The extinction of *D. stocki* was almost certainly related to the extinction of the Pleistocene megafauna in NA and the disappearance of its primary food source, possibly the blood of ground sloths or other large xenarthrans such as glyptodonts or pampatheres (Morgan, 1991; McDonald and Jefferson, 2008; Morgan et al., 2025).

Another extinct bat species described from San Josecito Cave is the big-eared bat *Corynorhinus tetralophodon* (family Vespertilionidae). According to Handley (1955, p. 48), *C. tetralophodon* differs from the two living species of *Corynorhinus*—C. *rafinesquii* and *C. townsendii*—by having the… "M3 with a well-developed fourth commissure [= postmetacrista], almost equaling the third commissure [= premetacrista] in length." However, in a catalog of the type specimens of vertebrates from San Josecito Cave, Arroyo-Cabrales and Johnson (2002) synonymized *C. tetralophodon* with *C. townsendii*, a species of big-eared bat that still lives in northern Mexico, because they found the M3 postmetacrista is variably present in *C. townsendii*.

Choate and Hall (1967) described two new extinct species of *Myotis*—*M. magnamolaris* and *M. rectidentis*—based on mandibles from the late Pleistocene Laubach Cave (now Inner Space Cavern) in Texas. Dorsey (1977) and Dalquest and Stangl (1984) reevaluated the taxonomic status of *M. magnamolaris* and concluded that this species was conspecific with the living cave myotis *M. velifer*. Dorsey (1977) also determined that *M. rectidentis* was a valid species. We tentatively follow Dorsey's (1977) recognition of *M. rectidentis*, but also point out that in our experience, mandibles of NA species of *Myotis* are difficult to separate at the species level, as also noted by Gaudin et al. (2011) and others, especially when sample sizes are small.

We present several examples of Pleistocene caves in the US that have produced notable samples of fossil bats, mostly based on our field and research experience. Late Quaternary deposits in Three-Forks Cave in the Ozark Highland, Adair County, eastern Oklahoma, produced a large sample of bats represented by over 800 bones and isolated teeth (Czaplewski et al., 2018). Skeletal elements of bats are by far the most common fossils in the Three-Forks Cave deposits, all pertaining to the Vespertilionidae, and most representing the genus *Myotis*. At least four species of bats occurred as fossils in Three-Forks Cave: big brown bat, *Eptesicus fuscus*; gray bat, *Myotis grisescens*; one smaller unidentified species of *Myotis*; and tricolored bat (also known as the eastern pipistrelle or American perimyotis), *Perimyotis* (formerly *Pipistrellus*) *subflavus*. Figure 2 illustrates examples of bat fossils preserved in Three-Forks Cave. Several of these bats, including *E. fuscus* and *M. grisescens*, are represented by juvenile individuals indicating this cave has been a maternity roost for those species since the late Pleistocene (Czaplewski et al., 2018). Despite the relatively large sample of bat fossils from Three-Forks Cave, intra- and interspecies variation in body size (as reflected in isolated skeletal elements) underscores the difficulty in identification of related species of bats. This is particularly true for the common and speciose genus *Myotis*; the identification of *M. grisescens* is largely based on the single intact cranium in Figure 2A. Two of the bats identified as fossils in Three-Forks Cave, *P. subflavus* and *M. grisescens*, are presently listed federally as endangered species. This cave is typical of late Pleistocene cave deposits from NA containing large samples of bats in which all of the species preserved are cave dwellers, members of the Vespertilionidae, and still live in the general vicinity of the cave. Schubert (2010) provided a radiocarbon date of 34,063 rcybp for a tooth of the short-faced bear, *Arctodus simus*, from Three-Forks Cave. In addition to *A. simus*, the presence of three other extinct Pleistocene megafauna, the ground sloth, *Megalonyx jeffersonii*; the dire wolf, *Canis* (= *Aenocyon*) *dirus*; and a horse (Equidae), support a late Pleistocene (Rancholabrean) age for the Three-Forks chiropteran fauna.

Carlsbad Caverns National Park (National Park Service acronym CAVE) in Eddy County, southeastern New Mexico, contains at least three caves with large samples of fossil bats of Pleistocene age—Carlsbad Cavern, Muskox Cave, and Slaughter Canyon Cave (Baker, 1963; Logan, 1981; Morgan and Lucas, 2006; Kottkamp et al., 2022). The bats from Slaughter Canyon Cave are discussed in the following section on early and middle Pleistocene (Irvingtonian) bat faunas from NA. A large colony of the Mexican free-tailed bat, *Tadarida brasiliensis*, consisting of approximately a quarter million individuals (CAVE website), still inhabits Carlsbad Cavern, the main tourist cave in CAVE (Fig. 3A). Figures 3B and 3C illustrate two complete articulated skeletons of bats of unknown age but presumably Late Quaternary, preserved in flowstone in Carlsbad Caverns. Baker (1963) first mentioned the presence of numerous bat fossils in Carlsbad Caverns with the largest samples in the so-called "scenic rooms," including the Papoose Room and Mystery Room. Figure 4A shows a large accumulation of skulls and disarticulated postcranial skeletons of bats in the Papoose Room (Photo from Baker, 1963, fig. 4). Figures 4B and 4C illustrate disarticulated skulls, mandibles, and limb bones of bats attached by flowstone to the wall of the cave in a vertical fissure deposit near the natural entrance to Carlsbad Caverns This site has not been dated

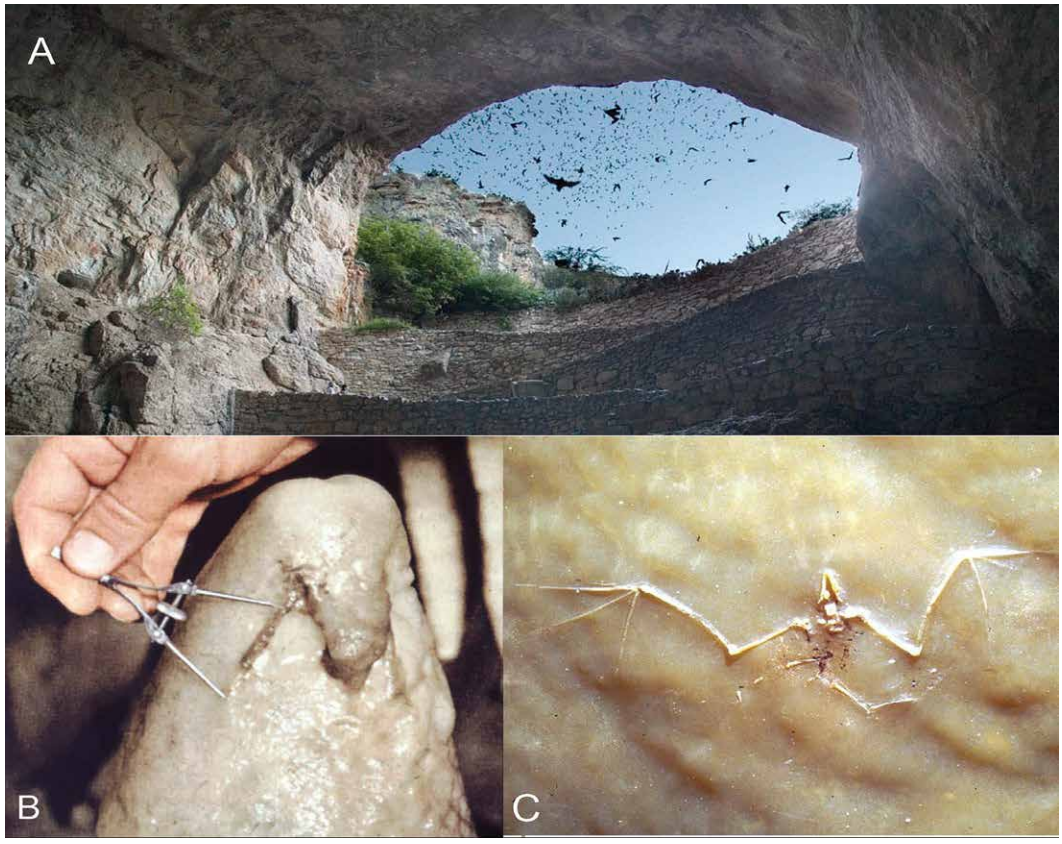

Figure 3. Carlsbad Cavern, Carlsbad Caverns National Park, Eddy County, New Mexico. (A) Carlsbad Cavern main entrance. Flight of Mexican free-tailed bats (*Tadarida brasiliensis*). (B, C) Bat skeletons preserved in flowstone, Carlsbad Cavern. (Photos courtesy of the National Park Service.)

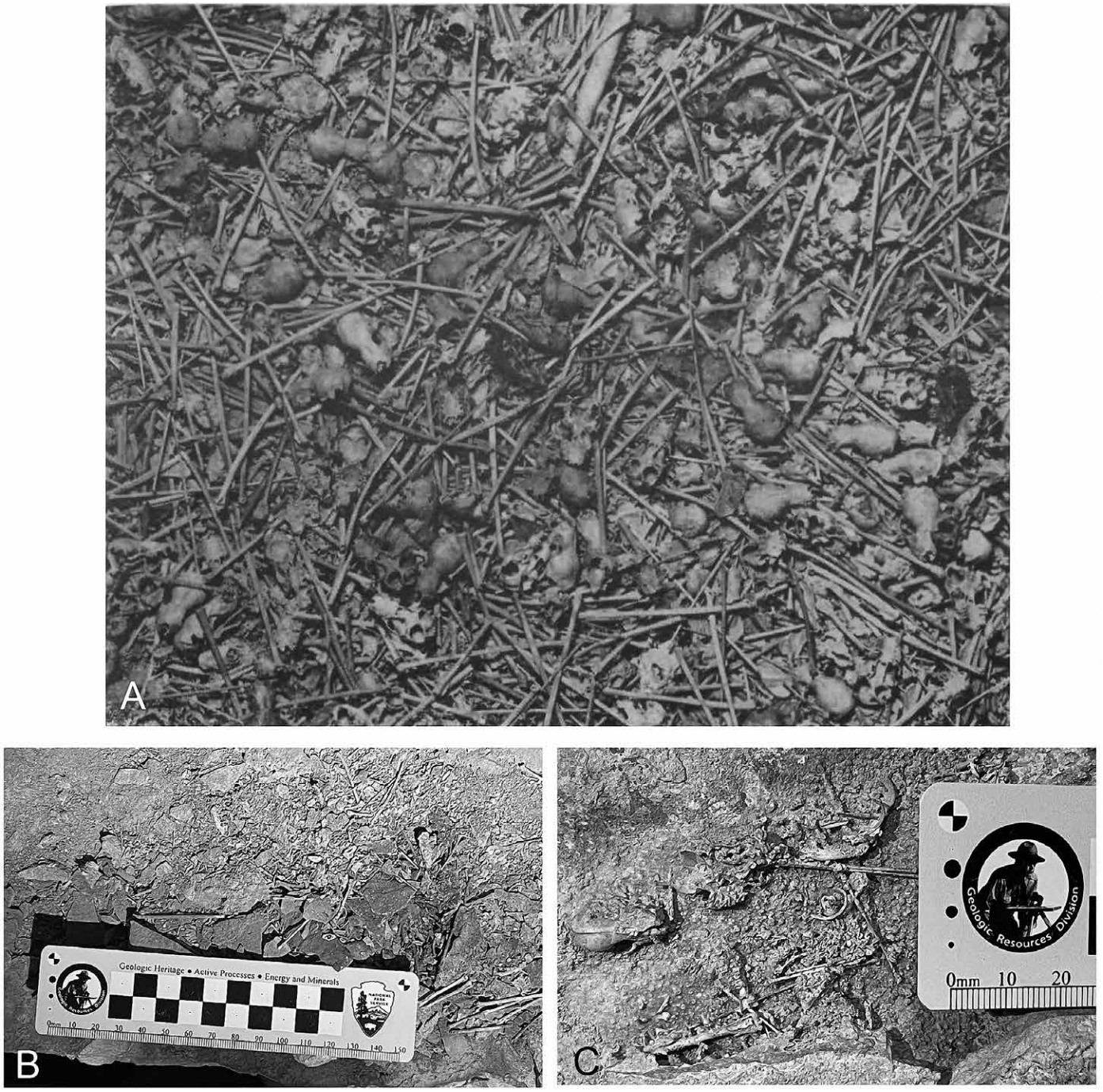

Figure 4. Carlsbad Cavern, Carlsbad Caverns National Park, Eddy County, New Mexico. (A) Accumulation of skulls and disarticulated skeletons of bats, Papoose Room (Photo from Baker, 1963). (B, C) Fossil bat skulls, mandibles, and limb bones (Vespertilionidae) in a vertical fissure deposit of Late Quaternary age near the natural entrance, attached to the cave wall with flowstone. (Photos courtesy of Rodney Horrocks (CAVE).)

but is probably late Pleistocene in age based on the discovery nearby of associated postcranial elements of the extinct American lion, *Panthera atrox* (Kottkamp et al., 2022). A locality in Lower Cave and another in the Big Room, both of which are in Carlsbad Cavern, contain guano deposits that have been radiocarbon-dated to approximately 50,000 rcybp and 35,000 rcybp, respectively (Jablonsky, NPS unpubl. reports, 1999, 2001; Kottkamp et al., 2022). These dates indicate that bats have inhabited Carlsbad Cavern for at least the past 50,000 years, if not considerably longer.

Muskox Cave has a sample consisting of several hundred partial skulls, mandibles, and limb bones of fossil bats, currently under study by GSM. Logan (1981) identified 6 species of bats from Muskox Cave, 5 vespertilionids—pallid bat, *Antrozous pallidus*; *Eptesicus fuscus*; *Myotis velifer*; fringed myotis, *Myotis thysanodes*; and Townsend's big-eared bat, *Plecotus* (=*Corynorhinus*) *townsendii*; and one molossid, *T. brasiliensis*, all living today in the Guadalupe Mountains

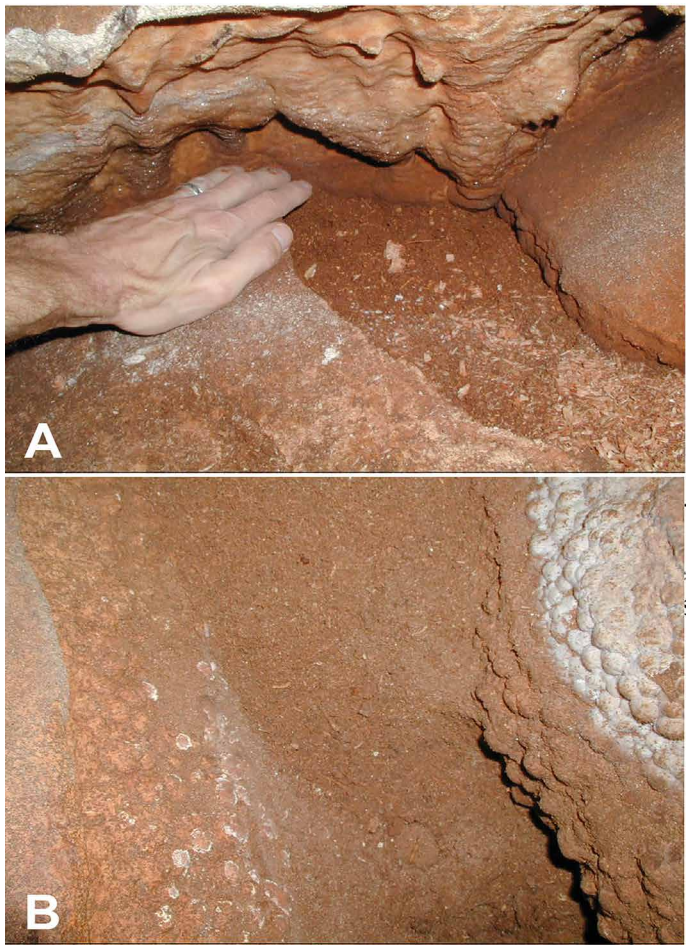

Figure 5. Quaternary deposit of bat bones in Arkenstone Cave, Arizona, including fringed myotis, *Myotis thysanodes*, and Stock's vampire bat, *Desmodus stocki.* (A) Excavation trench with a hand on the edge of the deposit. Several bones are visible as linear objects slightly paler than the bulk of the sediment. (B) Same trench, a closer view showing the pale linear bat limb bones and edentulous dentaries.

in southeastern New Mexico. Radiocarbon dates on collagen from fossil bones in Muskox Cave range from 18,140 to 25,500 rcybp, indicating an age corresponding with the Last Glacial Maximum (LGM).

Over 4,700 skeletal elements of bats were recovered from a small deposit of Quaternary sediment in Arkenstone Cave, Pima County, Arizona (Czaplewski and Peachey, 2003; Fig. 5). These bat fossils belong to three species in two families—*Myotis thysanodes* and a small unidentified species of *Myotis* represent the Vespertilionidae, and an extinct species, *Desmodus stocki*, represents the Phyllostomidae. Most of the fossils (>4,000) represent an attritional accumulation beneath a late Pleistocene maternity colony of *M. thysanodes*, with most of the bones representing juvenile individuals (Czaplewski and Peachey, 2003). Although *M. thysanodes* no longer roosts at the elevation of Arkenstone Cave (~1,110 m), this species still occurs in the same general vicinity in southern Arizona but at somewhat higher elevations (1,200–2,100 m). The bat bones are too leached to provide a radiocarbon date, and no other age-diagnostic mammals were recovered from this cave. However, other records of *D. stocki* are from the late Pleistocene (Ray et al., 1988), supporting a late Pleistocene (Rancholabrean) age for the Arkenstone Cave deposit.

Chiroptera from Early and Middle Pleistocene (Irvingtonian NALMA) Cave Deposits in the US

Although there are a number of late early Pleistocene and middle Pleistocene (Irvingtonian; ~0.25–1.0 Ma) cave deposits in the US (Kurtén and Anderson, 1980), there are fewer than late Pleistocene (Rancholabrean) cave sites. No vertebrate-bearing cave deposits are known in NA that are older than about 1 Ma. This includes the earliest portion of the Pleistocene (~1.0–2.6 Ma), corresponding to the late Blancan (~1.6–2.6 Ma) and very early Irvingtonian (~1.0–1.6 Ma) NALMAs. NA Irvingtonian cave sites that have produced significant samples of fossil bats include (Appendix): Cumberland Cave, Maryland (Gidley and Gazin, 1938; Eshelman et al., 2025); Hamilton Cave, West Virginia (Repenning and Grady, 1988; Grady, personal communication); Conard Fissure, Arkansas (Brown, 1908); Fyllan Cave, Texas (Winkler and Gose, 2003); Porcupine Cave, Colorado (Barnosky, 2004; GSM, NJC, personal observations); and Slaughter Canyon Cave, New Mexico (Morgan and Lucas, 2006; Kottkamp et al., 2022). Gidley and Gazin (1938) listed only two species of bats from the middle Pleistocene (medial Irvingtonian) Cumberland Cave, *Eptesicus grandis* and *Corynorhinus alleganiensis*, both supposedly extinct species. In a review of the Cumberland Cave vertebrate fauna, Eshelman et al. (2025) identified more than 1,000 specimens of bats and added 5 species to the faunal list, including 4 vespertilionids, 2 species of *Myotis*, *M. grisescens* and the eastern small-footed bat *M. leibii*, *Perimyotis subflavus*, the red bat *Lasiurus borealis*, and one molossid, *Tadarida* sp. Brown (1908) reported several hundred specimens of bats from the medial Irvingtonian Conard Fissure, describing the extinct subspecies *Eptesicus fuscus grandis* and identifying the genus *Myotis*. As indicated by the site name, Conard Fissure is a karst fissure deposit, much like those described from Florida, and is not a cave with an opening to the surface. Conard Fissure clearly was a cave in the middle Pleistocene, as observed by the abundance of bat fossils and the presence of well-developed cave formations (Brown, 1908).

Slaughter Canyon Cave in CAVE contains sediment, as much as 3 m or more in thickness, mostly consisting of an ancient bat guano deposit that supported a commercial guano mining operation in the early to mid-20th century (Baker, 1963; Morgan and Lucas, 2006; Kottkamp et al., 2022; Figs. 6A, B). Slaughter Canyon Cave contains a phenomenal sample of bat fossils numbering in the tens of thousands (Hundreds of thousands? Millions?), mostly representing the extinct Constantine's free-tailed bat, *Tadarida constantinei* (Figs. 6C-G). Lawrence (1960) described *T. constantinei*, distinguishing this species from the living *T. brasiliensis* by its significantly larger size and several cranial characters.

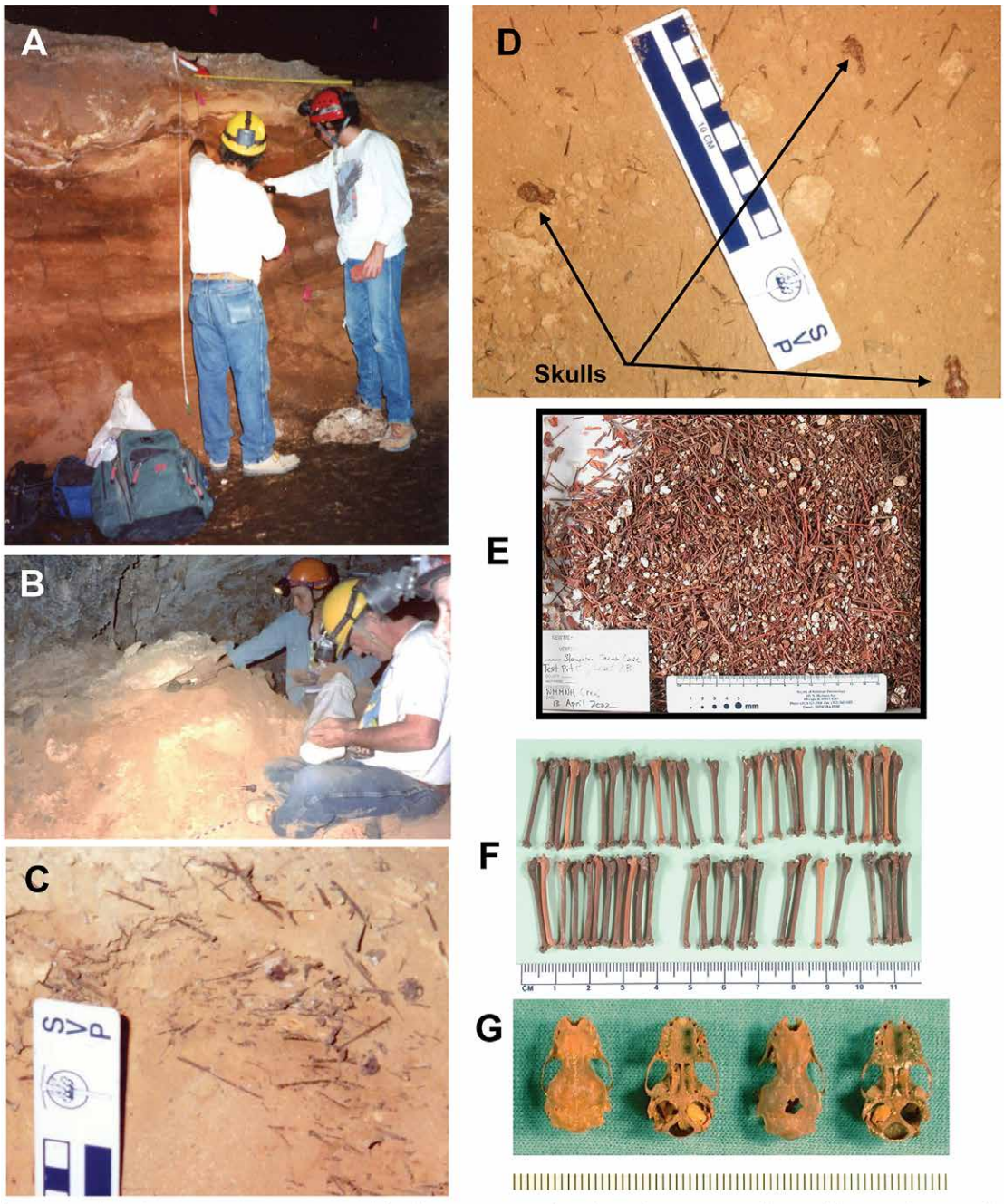

Figure 6. Slaughter Canyon Cave, Carlsbad Caverns National Park, New Mexico. This cave has produced a huge sample of bat fossils numbering in the tens of thousands of the extinct free-tailed bat, *Tadarida constantinei*, of middle Pleistocene age (Irvingtonian NALMA). (A) GSM (left) and Rick Toomey (right) measuring a section of ancient bat guano. (B) GSM (front) collecting a sample of *T. constantinei* fossils. Glenda Dawson (back) points to an overlying flowstone deposit with a U-series date of 206 to 212 ka. (C, D) In-place fossils of *T. constantinei*, including several skulls. (E) Sample of screenwashed concentrate from one bag of sediment (~10 kg) containing hundreds of bat fossils. (F) 50 complete humeri of *T. constantinei* from a single bag of sediment. (G) Four complete skulls of *T. constantinei*. (Photos in A-D courtesy of Patty Daw.)

Another factor supporting *T. constantinei* as a separate species is the presence in the Slaughter Canyon Cave deposits of a smaller species of *Tadarida* that appears to be conspecific with *T. brasiliensis* (Morgan and Lucas, 2006; Kottkamp et al., 2022). Although *T. constantinei* roosted in Slaughter Canyon Cave in large numbers in the middle Pleistocene, much like the modern colony of *T. brasiliensis* in Carlsbad Cavern, no bats have been observed roosting in this cave at present. Small numbers of fossils representing *Eptesicus fuscus* and two species of *Myotis* have also been identified from Slaughter Canyon Cave. Uranium-series dating of a flowstone overlying the fossil deposits in Slaughter Canyon Cave produced ages of 209 ka (Lundberg and McFarlane, 2006) and 212 ka (Polyak et al., 2006a), and U-series dates on other associated cave formations from this cave indicate a middle Pleistocene age (~0.5 Ma) that corresponds with a late Irvingtonian age for *T. constantinei* and the remainder of the vertebrate fauna (Polyak et al., 2006a). Records of an unidentified species of *Tadarida* larger than living *T. brasiliensis* are known from the medial Irvingtonian Hamilton Cave (Repenning and Grady, 1988; Grady, personal communication) and from a guano deposit in Mammoth Cave, Kentucky dated at >50 ka (Jegla and Hall, 1962; Widga and Colburn, 2015).

Only a few North American cave faunas are early medial Irvingtonian in age (~0.8-1.0 Ma), including Hamilton Cave (Repenning and Grady, 1988), Fyllan Cave (Winkler and Gose, 2003), Porcupine Cave (Barnosky, 2004; Barnoksy and Bell, 2004; Friedmann and Raynolds, 2004); and San Antonio Mountain (SAM) Cave, New Mexico (Rogers et al.,

2000). Except for Hamilton Cave, paleomagnetic analyses of sediments in these caves document reversed polarity indicating referral to the Matuyama Chron, probably the uppermost reversed interval (subchron 1r.1r; 0.78–0.99 Ma). The biochronology of arvicoline (microtine) rodents from all four of these cave sites supports an early medial Irvingtonian age. Rogers et al. (2000, p. 96) reported "Chiroptera species indeterminate" from SAM Cave, a lava tube cave from high elevation (2,737 m) in the San Juan Mountains of northern New Mexico. Porcupine Cave in the Rocky Mountains of central Colorado also occurs at high elevation (2,900 m; Barnosky, 2004). Bats occur in several sites within Porcupine Cave but are unpublished. We have examined the Porcupine Cave bat sample, which consists of 56 specimens, mostly partial mandibles, maxillae, humeri, and other postcranial elements representing several species of *Myotis* that cannot be identified below the generic level. Winkler and Gose (2003) listed five species of bats from Fyllan Cave on the Edwards Plateau in central Texas, including *Pipistrellus* (*Perimyotis*) *subflavus* and another small unidentified vespertilionid, a "medium bat" similar in size to *Myotis velifer*, a molossid near *Tadarida brasiliensis*, and a larger bat similar in size to the hoary bat *Lasiurus* (*Aeorestes*) *cinereus*. Despite the name, Fyllan Cave is a karst deposit not a cave based on the site description and photos (Winkler and Gose, 2003), but it was almost certainly a functioning cave during the Irvingtonian when it was inhabited by bats.

Several extinct species of bats were described from Irvingtonian cave and karst deposits in NA, including the vespertilionids, *Eptesicus grandis* and *Corynorhinus alleganiensis*; the molossid, *Tadarida constantinei*; and the vampire bat *Desmodus archaeodaptes* from two early Irvingtonian karst deposits in Florida (see discussion below). *Eptesicus grandis* was originally described as the large, extinct subspecies *Eptesicus fuscus grandis* from Conard Fissure in Arkansas (Brown, 1908). Gidley and Gazin (1938) identified this species from Cumberland Cave in Maryland and elevated it to species status as *Eptesicus grandis*. Although Conard Fissure and Cumberland Cave are Irvingtonian in age, most other records of *E. grandis* are from late Pleistocene (Rancholabrean) cave deposits in the eastern US (Guilday, 1967). A detailed analysis of a remarkable sample of this species, consisting over 3,000 mandibles and nearly 90 partial skulls from the late Pleistocene Robinson Cave in Tennessee, led Guilday (1967) to synonymize *E. grandis* with the living NA species, *E. fuscus*. *Corynorhinus alleganiensis* was described from Cumberland Cave (Gidley and Gazin, 1933) and has not been reported from any other Pleistocene cave sites in NA. Although we tentatively regard *C. alleganiensis* as valid, this species has not undergone a rigorous taxonomic analysis.

Bats from Late Pleistocene Cave Deposits in Mexico and Central America

Arroyo-Cabrales and Polaco (2008) reviewed the fossil record of bats from Mesoamerica, documenting 17 sites, including 15 sites from Mexico, 1 from Belize, and 1 from El Salvador. Among these 17 sites, 12 are from caves and 5 are from open sites. All 12 of the cave sites, 11 from Mexico and 1 from Belize, are late Pleistocene (Rancholabrean) in age. Several of the late Pleistocene cave deposits from Mexico contain important and diverse samples of fossil bats (Appendix; Arroyo-Cabrales and Polaco, 2003, 2008). Nine species of bats were reported from San Josecito Cave in the state of Nuevo León in northeastern Mexico (Jones, 1958; Arroyo-Cabrales and Polaco, 2003, 2008). San Josecito Cave is the type locality of the large extinct vampire bat, *Desmodus stocki*, and the extinct big-eared bat, *Corynorhinus tetralophodon*, and has also produced a large sample of the Mexican long-nosed bat, *Leptonycteris nivalis*, a nectarivorous bat that feeds on the flowers of large columnar cacti and agaves (Handley, 1955; Jones, 1958). Both *D. stocki* and *L. nivalis* are in the endemic New World family Phyllostomidae, most species of which occur in the Neotropical region. Arroyo-Cabrales and Johnson (2008) synonymized *Corynorhinus tetralophodon* with the living species *C. townsendii*, that still lives in the general vicinity of San Josecito Cave, as does a newly named extant species, *Corynorhinus leonpaniaguae*, recently separated from *Corynorhinus mexicanus* (López-Cuamatzi et al., 2024). Cueva de la Boca in Nuevo León, Cueva de la Presita in San Luis Potosí, and a cave near Tlapacoya in the state of Mexico have also produced specimens of *D. stocki* (Ray et al., 1988; Arroyo-Cabrales and Polaco, 2003, 2008).

The late Pleistocene chiropteran fauna from Cueva de El Abra in the state of Tamaulipas in northeastern Mexico consists of 9 species, including several tropical forms typical of southern Mexico and Central America (Dalquest and Roth, 1970; Arroyo-Cabrales and Polaco, 2003, 2008). This cave is in the tropical lowlands of southeastern Tamaulipas, a region that documents the northernmost range of many species of Neotropical bats (Ceballos et al., 2014). Four species of Neotropical bats are represented by fossils from Cueva de El Abra, the emballonurid *Balantiopteryx io*, the frugivorous phyllostomid *Artibeus jamaicensis*, and the molossids *Nyctinomops aurispinosus* and *N. laticaudatus*. *B. io* from Cueva de El Abra represents one of the few extralimital records of bats from late Pleistocene cave deposits in Mexico, as this species now occurs no farther north than central Veracruz, several hundred kilometers south of Cueva de El Abra.

Two caves on the Yucatán Peninsula produced diverse samples of Late Quaternary bats: Loltún Cave or Gruta de Loltún in the state of Yucatán in Mexico (Arroyo-Cabrales and Alvarez, 2003; Arroyo-Cabrales and Polaco, 2003, 2008) and Cebada Cave in Belize (Czaplewski et al., 2003a). Most of the bats from Loltún Cave (15 species) and Cebada Cave (9 species) consist of tropical species that still inhabit southern Mexico and northern Central America. One

notable exception is that both caves contain fossils of the giant extinct vampire bat, *Desmodus draculae*, a tropical species also recorded from caves in Venezuela and Brazil (Morgan et al., 1988; Czaplewski and Cartelle, 1998). Both *D. draculae* and *D. stocki* presumably fed upon the blood of one or more species of large mammals, possibly ground sloths, and became extinct at the end of the Pleistocene when their food sources also became extinct (Morgan, 1991; McDonald and Jefferson, 2008). These two extinct vampire bats have differing sizes: *D. draculae* is significantly larger than *D. stocki* and both species are larger than living *D. rotundus*. Together with their non-overlapping geographic ranges, *D. draculae* is restricted to the Neotropics from southern Mexico south to Brazil and *D. stocki* occurs from central Mexico to the southern US, this apparently reflects a difference in their prey species and perhaps their differing abilities to tolerate cooler temperatures.

Except for Cebada Cave, fossil bats are not reported from any other Pleistocene cave deposits from Belize and Guatemala south to Panama, in part owing to the overall rarity of caves in the predominantly volcanic terrane of Central America (Fig. 1B). Churcher (2020) reported a late Pleistocene (Rancholabrean) fauna from Extinction Cave in Belize, containing several extinct species of large mammals, including *Dasypus bellus*, *Panthera atrox*, *Tremarctos floridanus*, and *Equus conversidens*. However, the fauna from Extinction Cave did not include any bats or other small mammals, suggesting the site was not screened for microvertebrates. We suspect there are other caves with undiscovered late Pleistocene bat fossils from the carbonate terrain of Belize and northern Guatemala that forms the southeastern portion of the Yucatán Peninsula, probably including cenotes or underwater caves. Several fairly extensive cave systems are known from Central America, for example, Candelaria Caves and Grutas de Lanquín in Guatemala, Talgua Cave in Honduras, Terciopelo Cave and Venado Cave in Costa Rica, and Bayano Cave in Panama. However, to our knowledge, none of these caves have been systematically explored for Pleistocene vertebrate fossils. Pleistocene mammal faunas are known from most countries in Central America, including: Guatemala (Dávila et al., 2019; Lucas et al., 2021), Honduras (Webb and Perrigo, 1984; Lucas, 2008), El Salvador (Webb and Perrigo, 1984; Cisneros, 2005, 2008), Nicaragua (Lucas et al., 2008), Costa Rica (Lucas et al., 1997), and Panama (Gazin, 1957; Pearson, 2005; Lucas, 2014). However, these Central American Pleistocene faunas are mostly derived from open sites and mostly consist of large mammals, with no records of fossil bats. Webb and Perrigo (1984) illustrated a partial articulated skeleton tentatively identified as *Pteronotus parnellii* from the early Pleistocene (early Irvingtonian) Barranca del Sisimico LF in El Salvador. Although *P. parnellii* is member of the Mormoopidae and most species in this family are obligate cave dwellers (Smith, 1972), the skeleton from Barranca del Sisimico was derived from a diatomite representing a former lake deposit (Webb and Perrigo, 1984).

Chiroptera from Late Pleistocene and Holocene Cave Deposits in the West Indies

The West Indian islands have a remarkably robust record of fossil bats from cave deposits (Appendix; Morgan, 2001; Dávalos and Turvey, 2012) that date to the Late Quaternary (late Pleistocene or Holocene). Caves are abundant throughout Cuba, Jamaica, Hispaniola, and Puerto Rico, as well as the Bahamas and Cayman Islands, where widespread exposures of Cretaceous and Cenozoic carbonate rocks have been eroded into an extensive karst topography. This includes several hundred cave sites that have yielded Late Quaternary bats and other vertebrate fossils (Morgan and Woods, 1986; Morgan, 2001; Dávalos and Turvey, 2012). Abundant and diverse samples of Late Quaternary bats are known from caves on all four of the large Greater Antillean islands, including (Appendix): Cuba (Silva Taboada, 1974; 1979); Jamaica (Koopman and Williams, 1951; Morgan, 1993); Hispaniola (Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017), and Puerto Rico (Anthony, 1917, 1918, 1925; Choate and Birney, 1968). Substantial Late Quaternary bat faunas are also known from several smaller islands in the West Indies, including (Appendix): Abaco, Andros, and New Providence in the Bahamas (Morgan, 1989, 2001; Steadman et al., 2007; Soto-Centeno and Steadman, 2015); Grand Cayman and Cayman Brac in the Cayman Islands (Morgan, 1994); and Antigua (Steadman et al., 1984; Pregill et al., 1988) and Marie Galante in the Lesser Antilles (Stoetzel et al., 2016). Late Quaternary cave deposits in the West Indies have a much more diverse fossil record of the Chiroptera than does Mesoamerica. Furthermore, the Late Quaternary Antillean chiropteran fauna has also undergone more extensive extinctions and extirpations (local extinctions or island population losses) than in the late Pleistocene of continental North America.

The combined extant and Late Quaternary chiropteran fauna of the West Indies consists of 70 species (Appendix; Varona, 1974; Baker and Genoways, 1978; Silva Taboada, 1979; Koopman, 1989; Morgan, 2001; Tejedor, 2011; Dávalos and Turvey, 2012; Pavan and Marroig, 2016). Eight of these (11% of the bat fauna) are extinct species known only as Late Quaternary fossils: *Mormoops magna* and *Pteronotus pristinus* in the Mormoopidae; and *Artibeus anthonyi*, *Cubanycteris silvai*, *Phyllonycteris major*, *Phyllops silvai, Phyllops vetus,* and *Tonatia saurophila* in the Phyllostomidae. Four of these 8 extinct species, *A. anthonyi*, *C. silvai*, *P. silvai,* and *P. vetus,* are known only from Cuba (Woloszyn and Silva Taboada, 1977; Silva Taboada, 1979; Suárez and Diaz-Franco, 2003; Mancina and Garcia-Rivera, 2005). *Mormoops magna* occurred on both Cuba and Hispaniola (Silva Taboada, 1974; Velazco et al., 2013). *Pteronotus pristinus* was described from Cuba (Silva Taboada, 1974) and tentatively identified from a late Pleistocene karst deposit in southernmost Florida (Morgan, 1991). *Tonatia saurophila* is known only from Jamaica (Koopman and Williams, 1951).

Phyllonycteris major was originally described from Puerto Rico (Anthony, 1917, 1918) and has since been identified from two caves in the Lesser Antilles: a late Holocene cave deposit in Burma Quarry in Antigua (Pregill et al., 1988) and Holocene and late Pleistocene deposits from Blanchard Cave in Marie Galante (Stoetzel el al., 2016). *Tonatia saurophila* has a complicated taxonomic history, originally described as an extinct species known only from two caves in Jamaica (Koopman and Williams, 1951). Later, the name *T. saurophila* was applied to both the Jamaican fossils and a living species on the mainland, originally referred to the *T. bidens* complex, that occurs from Mexico to South America (Williams et al., 1995). Recently, two of the mainland forms in the *Tonatia bidens* complex, *T. bakeri* from Mexico and Central America and *T. maresi* from South America, were elevated to full species and *T. saurophila* was returned to its original status as an extinct species restricted to Late Quaternary cave deposits from Jamaica (Basantes et al., 2020). The eight extinct species of bats from the West Indies document more than twice the number of late Pleistocene bat extinctions that occurred in the far larger area of continental North America, from the US and Canada south to Panama, consisting of only three species: two species of vampire bats, *Desmodus draculae* and *D. stocki*; and the vespertilionid, *Myotis rectidentis*.

The West Indies experienced even more extensive extirpations of bat species, with 18 living species (29% of the extant Antillean bat fauna of 62 species) known to have undergone local extinction on one or more islands. Among those 18 species, two disappeared from the West Indies but still survive in Mesoamerica—a mormoopid, the ghost-faced bat *Mormoops megalophylla*; and a phyllostomid, the vampire bat, *Desmodus rotundus*. *M. megalophylla* has the most extensive West Indian distribution of these two species, with extirpated populations from Late Quaternary cave deposits in Cuba, Jamaica, Hispaniola, Abaco and Andros in the Bahamas, and Marie Galante in the Lesser Antilles (Silva Taboada, 1974; Morgan, 1989, 1993, 2001; Stoetzel et al., 2016), as well as peninsular Florida (Morgan, 1991, 2002). *D. rotundus* has been recorded in the West Indies from five Late Quaternary cave deposits in Cuba (Orihuela, 2011). A third extirpated species no longer found in the West Indies is a vespertilionid, the southeastern myotis, *Myotis austroriparius*, now restricted to Florida and the southeastern US, but tentatively identified from three Late Quaternary cave deposits on Abaco in the northern Bahamas (Morgan, 2001; Soto-Centeno and Steadman, 2015). There are currently no living species of *Myotis* found in the Greater Antilles or Bahamas. The identification of *M. austroriparius* from Abaco requires further study; as noted above, fragmentary fossils of *Myotis* are notoriously difficult to identify to species.

Among the other 15 West Indian bat species with extirpated populations on one or more islands, most of these occurred on smaller islands, including Abaco, Andros, and New Providence in the Bahamas; Grand Cayman and Cayman Brac in the Cayman Islands; and Anguilla, Antigua, Barbuda, and Marie Galante in the Lesser Antilles (Morgan, 2001). More than half of the species (8) that suffered local extinctions in the West Indies belong to two families of obligate cave-dwelling bats that reach their highest modern species diversity in the West Indies, Mormoopidae and Natalidae. Four of the 7 living species of mormoopids in the West Indies are known from one or more locally extinct populations, including the Antillean ghost-faced bat, *Mormoops blainvillei*, from caves on 8 islands where this species no longer occurs and 7 extirpated populations of Parnell's mustached bat, *Ptenonotus parnellii*. Four of the 8 extant species of Natalidae in the West Indies are also represented by extirpated island populations, including 7 locally extinct populations of a large species of funnel-eared bat previously referred to as either *Natalus stramineus* or *N. major*. Varona (1974) and Koopman (1989) recognized a single species of large *Natalus* in the West Indies, *N. stramineus*, whereas Morgan (2001) referred the large *Natalus* from the Greater Antilles to *N. major*. In a systematic review of the Natalidae, Tejedor (2011) recognized 3 large species in this genus from the Greater Antilles—*N. jamaicensis* from Jamaica, *N. major* from Hispaniola, and *N. primus* from Cuba, and restricted *N. stramineus* to the Lesser Antilles. Fossils representing extirpated populations of a large species of *Natalus* from Abaco, Andros, New Providence, Middle Caicos, and Grand Cayman were previously referred to *N. major* (Morgan, 2001). Following the systematic revision of the Natalidae (Tejedor, 2011), further study is required to determine the correct species identifications of the extirpated populations of a large *Natalus* in the Bahamas, Caicos Islands, and Cayman Islands. Several West Indian species in the Phyllostomidae also underwent rather widespread extirpations, including Waterhouse's leaf-nosed bat, *Macrotus waterhousii*, and the Greater Antillean long-tongued bat, *Monophyllus redmani*, both identified from fossils on five islands where these species no longer occur, and the Cuban fruit-eating bat *Brachyphylla nana* that became extinct on four islands.

The widespread disappearances of bats from certain islands in the West Indies during the Late Quaternary, including both species-level losses (extinctions) and population-level losses (extirpations), have been attributed to several causes, including reduction in island size as a result of rising sea level in the late Pleistocene, especially on smaller islands with low topography (e.g., Bahamas), flooding of low-lying caves also caused by rising sea level, and natural changes in climate and habitat (i.e., not human caused), most of which would have occurred during the late Pleistocene-Holocene transition from 11–9 ka (Morgan, 1999, 2001; Dávalos and Russell, 2012; Soto-Centeno and Steadman, 2015). Rising sea level and the flooding of caves that were dry during the late Pleistocene low sea level stand were certainly factors, as several underwater caves, also known as "blue holes" in the Bahamas, have produced samples of bat fossils, including Dan's Cave, Ralph's Cave, and Sawmill Sink on Abaco (Steadman et al., 2007; Soto-Centeno and Steadman, 2015; Fig. 7A) and

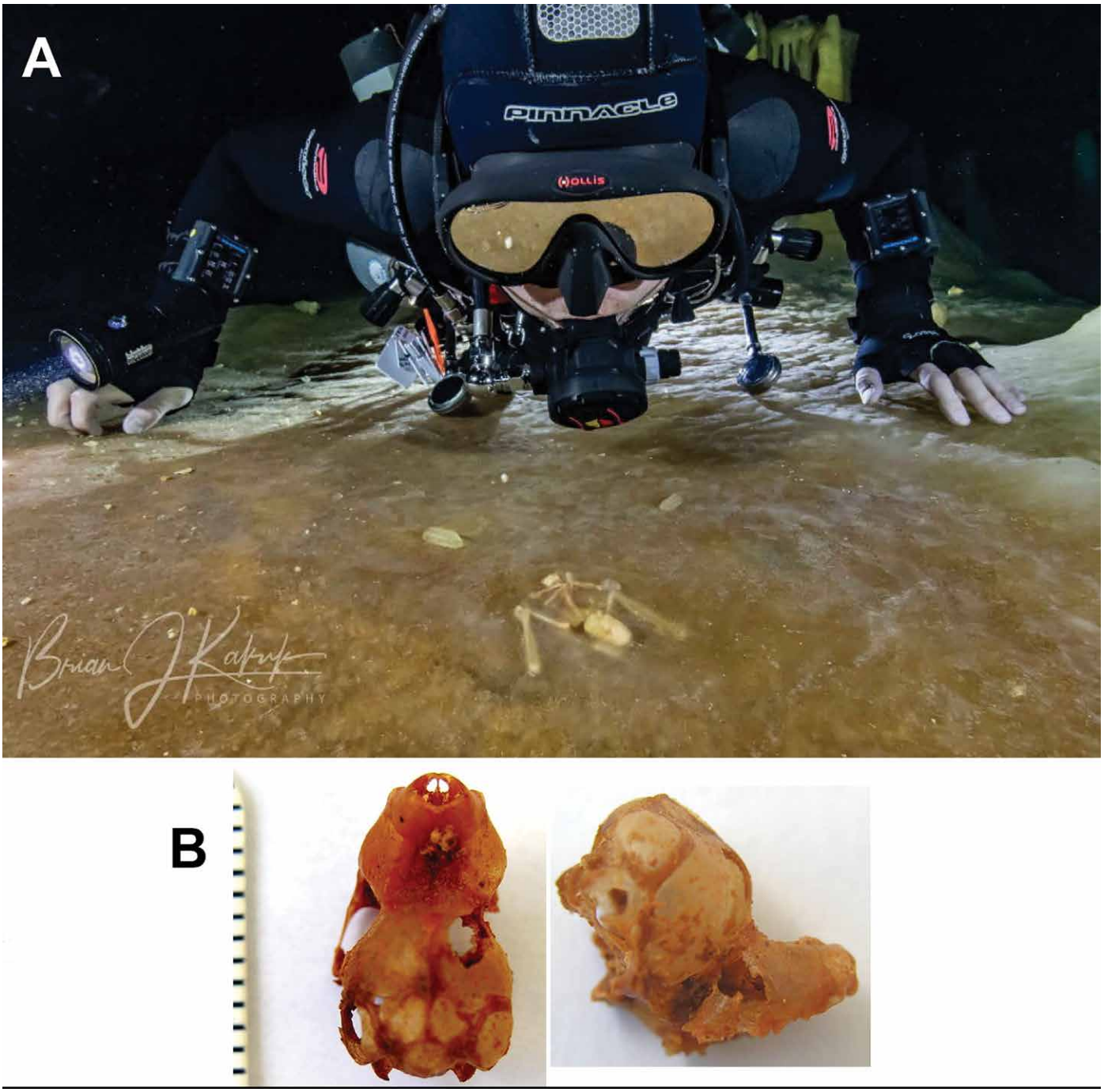

Figure 7. (A) Cave diver examining an articulated skeleton of a bat preserved in clear flowstone at a depth of 16 meters (52 feet) and a distance of 218 meters (715 feet) from the cave entrance, Ralph's Cave, Abaco, Bahamas (Photo courtesy of Brian J. Kakuk). (B) Fossil skull of a mormoopid bat, *Mormoops blainvillei*, dorsal view (left), lateral view (right), collected at depth of 18 meters and a distance of 91 meters from the cave entrance, Dan's Cave, Abaco, Bahamas. *Mormoops blainvillei* is now extralimital to the Bahamas (Skull photos courtesy of Nancy Albury).

Oleg's Bat Cave and Cueva de Lily in the Dominican Republic (Velazco et al., 2013; Fig. 8). Sawmill Sink produced four species of bats, including the vespertilionid, *Myotis austroriparius*, that no longer occurs in the Bahamas, from an owl roost deposit at a depth of 27–35 m below modern sea level. Bones from the owl roost in Sawmill Sink lack collagen so cannot be radiocarbon dated; however, the presence of a diverse terrestrial vertebrate fauna, including bats, birds, snakes, and lizards, at a depth of 35 m clearly indicates a late Pleistocene age older than 11 ka (Steadman and Franklin, 2015). Figure 7B illustrates a complete skull of the mormoopid bat, *Mormoops blainvillei*, now extirpated from the Bahamas, recovered from the floor of Dan's Cave on Abaco at a depth of 18 m and a distance of 91 m from the cave entrance. Although this skull has not been radiocarbon dated, *M. blainvillei* is an obligate cave dwelling bat that obviously inhabited Dan's

Figure 8. Flooded floor of Oleg's Bat Cave in the Dominican Republic, where numerous bat cranial and postcranial remains can be observed. Bat fossils were collected at this site from a depth of 8 m and about 15 m from the cave entrance (Photograph courtesy of Phillip Lehman. Reproduced from Velazco et al., 2013, with permission of the AMNH).

Cave when it was a dry cave during a period of lower sea level in the late Pleistocene. Dan's Cave also contains extensive cave formations (stalactites, stalagmites, etc.) that form only under subaerial conditions but are now 18 m or more underwater. Fossils representing five extirpated species of bats from Ralph's Cave on Abaco, including three obligate cave dwellers, *Pteronotus parnellii*, *Monophyllus redmani*, and *Natalus primus*, late Holocene in age, with AMS radiocarbon dates ranging from 1,820 to 4,220 YBP (Soto-Centeno and Steadman, 2015). These dates are considerably younger than the major rise in sea level and changes in climate and vegetation that occurred during the late Pleistocene to the early Holocene transition (between 11 and 9 ka), suggesting these local bat extinctions were probably related to the arrival of humans and subsequent habitat changes in the Bahamas in the late Holocene (Soto-Centeno and Steadman, 2015). Oleg's Bat Cave in the Dominican Republic produced a remarkable sample of Late Quaternary bats, with 11 species represented by thousands of fossils, including hundreds of complete skulls recovered from the cave floor 8 m underwater and about 15 m from the cave entrance (Fig. 8). The bat fauna from Oleg's Bat Cave includes one extinct species, *Mormoops magna*, otherwise known only from Cuba, and one species that no longer occurs on Hispaniola, *Pteronotus macleayii* (Velazco et al., 2013); both are mormoopids, a family in which almost all living species are obligate cavernicoles (Smith, 1972; Morgan et al., 2019).

FOSSIL BATS FROM CENOZOIC CAVE AND KARST DEPOSITS IN FLORIDA

Fossil bats from cave and karst deposits in Florida are treated in a separate section because the record consists primarily of fossils from karst deposits not caves. The Florida record also covers a much longer period of time than elsewhere in North America, beginning in the early Oligocene (~30 Ma) and extending to the end of the Pleistocene (10 ka). The region that is now the Florida peninsula was submerged until the Oligocene, and as a result, much of northern peninsular Florida is underlain by Eocene and Oligocene marine limestones. Florida first emerged above sea level in the early Oligocene, and throughout the remainder of the Cenozoic, the peninsula fluctuated between submerged and emergent depending upon changes in 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). The map in Figure 9 shows the distribution of limestone in Florida and the associated karst terrain. Areas with limestone at or near the surface (in red) have well developed karst solution features, as do areas with a moderate covering of clastic sediments (in gold). Most of the cave and karst fossil deposits in Florida are located in the areas of either red or gold on this map.

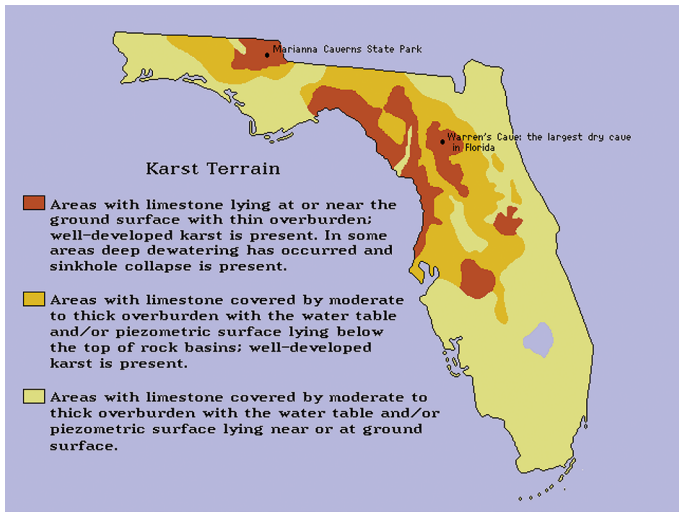

Figure 9. Map of Florida showing the karst terrain. Most Florida fossil faunas containing abundant bats are former cave deposits and are located in areas with well-developed karst (indicated by red and gold on this map). (Map courtesy of the Florida Speleological Society.)

The north Florida karst geomorphic province is well known for the abundance of fossil deposits containing

terrestrial vertebrates occurring in current or former caves and other paleokarst features (Morgan and Hulbert, 2008). Karst deposits of terrestrial origin generally consist of sands and clays filling solution features such as sinkholes, fissures, and isolated sediment pockets, and often contain large samples of both small and large terrestrial vertebrates. The presence of bat fossils in many of these karst deposits is especially diagnostic, suggesting they represent the remnants of former cave systems. The same erosional processes that originally formed caves in the Florida peninsula eventually destroyed most of them. With the collapse of the caves, their contained sediments and fossils became buried, and the caves were no longer accessible from surface entrances. The limestones in northern Florida are mined commercially for road bedding and other construction purposes, which has resulted in the discovery of most of these karst fossil deposits. Vertebrate paleontologists from the Florida Museum of Natural History (FLMNH) regularly survey active commercial limestone mines in search of clay- and sand-filled fissures and sinkholes containing fossils (Fig. 10). 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, 2023). Nowhere else in North America are karst-derived vertebrate fossil deposits of Cenozoic age found in such abundance in a limited geographic region. Moreover, we suspect only a small percentage of these buried fossiliferous karst deposits have been uncovered within the past century through mining operations.

Chiroptera from Late Pleistocene (Rancholabrean) Cave and Karst Deposits in Florida

The process of cave formation and destruction/collapse in Florida appears to have occurred rather rapidly in geologic time. Dry caves in Florida containing surficial deposits that have produced vertebrate fossils are exclusively late Pleistocene in age (<250 ka) and are referred to the Rancholabrean based on the presence of *Bison* or other mammals typical of this NALMA (Morgan and Hulbert, 1995). Late Pleistocene subaerial cave sites (i.e., not underwater) containing vertebrate fossils that retain an opening to the surface, fitting the definition of a cave, are not numerous in Florida, including fewer than 10 sites, the best known of which are: Surprise Cave, Alachua County; Eichelberger Cave and Mefford Cave, Marion County; and Saber-tooth Cave, Citrus County, all located in the Florida peninsula; and Peccary Tooth Cave near Florida Caverns State Park in Jackson County in the Florida panhandle (Simpson, 1928; Webb, 1974; Morgan and Hulbert, 2008; Gillette and Means, personal communication). Only two of those cave sites, Surprise Cave and Peccary Tooth Cave, contain substantial bat faunas (Appendix). The fossil bats from these caves mostly consist of vespertilionids that still occur in Florida, although the presence of the gray bat *Myotis grisescens* in Surprise Cave is extralimital, about 300 km southeast of the southernmost current record of this species in Jackson County in the Florida panhandle (Marks and Marks, 2006).

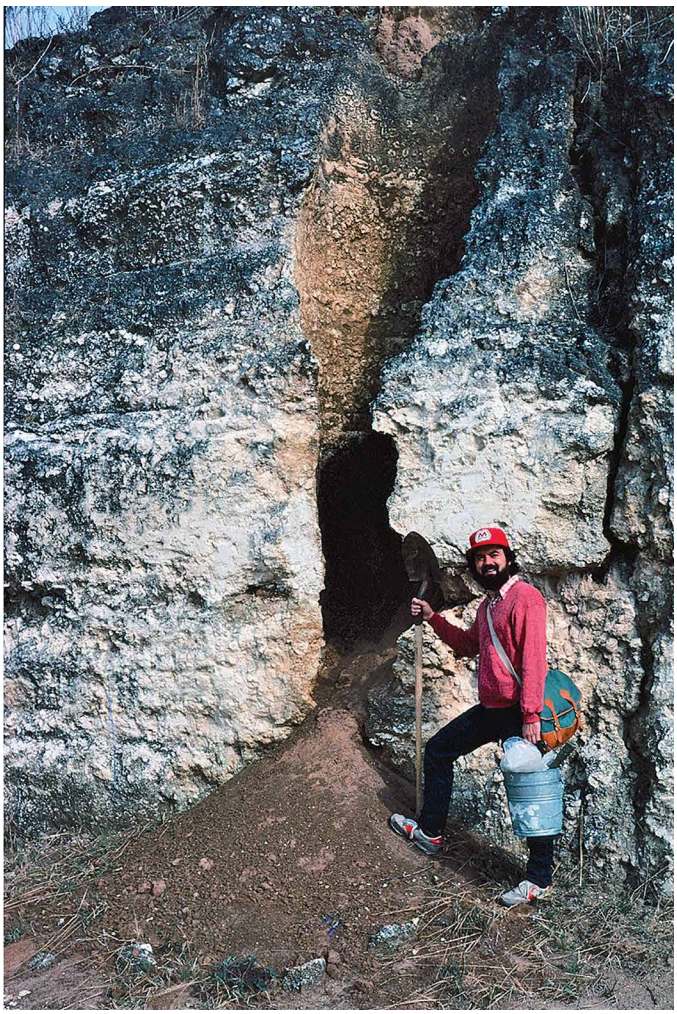

Figure 10. Karst fissure deposit, Haile Quarry complex, Alachua County, Florida. Reddish brown sands and clays deposited in a former cave contained late Pleistocene vertebrate fossils, including bats. The fissure is formed in the marine Eocene Ocala limestone. GSM for scale.

Groundwater levels are generally high in Florida and many caves are submerged (Scott et al., 2004). No dry caves currently occur in the southern third of the Florida peninsula and the Florida Keys (Morgan, 2002). Many of these underwater caves and springs would have been subaerial during the late Pleistocene low sea level stand (maximum of ~120 m below current sea level) that corresponded with lower regional water tables. Sea level began rising in the late Pleistocene and reached its current level in the early Holocene, flooding many previously dry caves and cave/spring complexes in Florida. Underwater caves greatly outnumber dry caves in northern Florida (Scott et al., 2004). Beginning in the 1960s, paleontologists from the FLMNH began working with scuba divers throughout northern Florida to recover vertebrate fossils from rivers, springs, underwater caves, and water-filled sinkholes (Webb, 1974). These underwater sites have mostly produced large vertebrates, but a few are known to contain late Pleistocene deposits with bats, including Devil's Den in

Levy County (Martin and Webb, 1974) and Rock Springs in Orange County (Ray et al., 1963; Wilkins, 1983). Both sites were subaerial caves when they were inhabited by bats in the late Pleistocene during a period of lower sea level and correspondingly lower regional water tables.

In the early 1960s, scuba-diving paleontologists H. K. Brooks and Clayton Ray recovered late Pleistocene vertebrates in Devil's Den, a water-filled sinkhole/cave complex with a lateral passage at about 20 m in depth. Devil's Den has produced a large sample of Rancholabrean fossils, in particular several skeletons of the extinct Florida cave bear, *Tremarctos floridanus* (Kurtén, 1966), as well as four species of bats, *Myotis* cf. *austroriparius*, *M. grisescens*, *Pipistrellus* (*Perimyotis*) *subflavus*, and yellow bat cf. *Lasiurus* (*Dasypterus*) *intermedius* (Martin and Webb, 1974). As with the record of *M. grisescens* from Surprise Cave, the Devil's Den record of the gray bat is several hundred kilometers south and east of its current southernmost occurrence in the Florida Caverns area near Marianna in the Florida panhandle (Marks and Marks, 2006). In 1957, Jack Todd recovered fossil vertebrates from Rock Springs, an underwater spring and cave complex (Ray et al., 1963; Wilkins, 1983; Morgan, 1991, 2002). Rock Springs has produced over 25 species of both small and large mammals (Wilkins, 1983) and a remarkable sample of fossil birds, with over 1,000 specimens representing 35 species (Woolfenden, 1959). Rock Springs has produced two species of cave-dwelling bats, the extralimital mormoopid, *Mormoops megalophylla*, and *Myotis austroriparius*. *M. megalophylla* is no longer found in Florida or elsewhere in the eastern US. It is primarily a tropical American species, occurring as far north as southwestern Texas. We are certain that further exploration of underwater caves in Florida will continue to yield important samples of fossil vertebrates, including bats.

More than 25 separate late Pleistocene karst deposits have been documented from the Haile Quarry complex in Alachua County, northern peninsular Florida, an area covering several square kilometers with more than 20 commercial limestone quarries. FLMNH paleontologists have assigned each of these quarries a number (e.g., Haile 7), and within a quarry each separate karst deposit is given a letter (e.g., Haile 7C is the third named karst deposit within Haile Quarry 7). The Haile Quarry complex also contains several older middle and early Pleistocene (Irvingtonian and Blancan) and late Miocene (Hemphillian) karst deposits containing vertebrate fossils (see next section). Other areas of the Florida peninsula with numerous fossiliferous late Pleistocene karst deposits include: Arredondo (11 sites) and Kanapaha (6 sites) in Alachua County; Reddick (7 sites) in Marion County; Lecanto (3 sites) in Citrus County; Coleman (5 sites) in Sumter County; and 2 sinkhole sites, Cutler Hammock and Monkey Jungle Hammock, in Dade County, southernmost peninsular Florida (Webb, 1974; Morgan. 1991, 2002; Emslie and Morgan, 1995; Morgan and Hulbert, 2008).

Florida late Pleistocene (Rancholabrean) karst deposits document several species of extinct and extralimital species of bats (Appendix), and in this regard, the Florida record bears more similarity to the Late Quaternary bat record of the West Indies than to the remainder of continental North America. The large extinct vampire bat, *Desmodus stocki*, occurs in four late Pleistocene karst deposits in northern peninsular Florida, Arredondo 2, Haile 1A, and Haile 11B in Alachua County; and Reddick 1 in Marion County (Morgan, 1991). This large vampire bat was originally described as *Desmodus magnus* from Reddick 1 (Gut, 1959), but has since been shown to be a synonym of *D. stocki* (Hutchison 1967; Morgan, 1991), described the previous year from San Josecito Cave in northern Mexico (Jones, 1958), and also known from about a dozen other late Pleistocene caves sites in the southwestern US and Mexico (Ray et al., 1988). A second extinct species, the mormoopid, *Pteronotus pristinus*, occurs in Monkey Jungle Hammock, a late Pleistocene sinkhole deposit in southernmost Florida, (Morgan, 1991, 2002). *P. pristinus* is otherwise known only from Late Quaternary cave deposits in Cuba (Silva Taboada, 1974), and represents the only record of the tropical genus, *Pteronotus*, in the US. Late Pleistocene extralimital records of bats from Florida include two other primarily tropical species, the mormoopid, *Mormoops megalophylla*, and the large molossid, *Eumops underwoodi*. *M. megalophylla* has been identified from three Florida late Pleistocene karst-derived deposits, Rock Springs in Orange County in central Florida, an underwater cave, as described above (Ray et al., 1963; Wilkins, 1983; Morgan, 1991); and two karst sinkhole deposits, Cutler Hammock and Monkey Jungle Hammock in Dade County in the southernmost peninsula (Morgan, 1991, 2002). *M. megalophylla* no longer occurs in Florida, with the closest mainland (overland) population from southwestern Texas about 2,000 km west of Florida. As noted above, there are also six extirpated populations of *M. megalophylla* from the West Indies where this mainland Neotropical species also no longer occurs. It is possible (likely?) that the Florida late Pleistocene population of *M. megalophylla* dispersed from the West Indies, probably Cuba or the northern Bahamas (Abaco and Andros), which are only a few hundred kilometers east (Bahamas) or south (Cuba) of southern peninsular Florida. The origin of the extirpated populations of *M. megalophylla* from both Florida and the West Indies could eventually be determined through the analysis of ancient DNA. The Cutler Hammock and Monkey Jungle Hammock sinkholes were both part of extensive cave systems in the late Pleistocene based on the abundance of cavernicolous bats in these deposits, including the vespertilionids, *Eptesicus fuscus* and *Myotis austroriparius*, and the mormoopids, *M. megalophylla* and *P. pristinus* (Morgan, 1991, 2002). These two vespertilionids no longer occur in the southern third of the Florida peninsula because they require caves for roosting, and this region now lacks dry caves. A living species of a large molossid, Underwood's bonneted bat, *Eumops underwoodi*, was identified from Lecanto 2A, a late Pleistocene karst deposit in central Florida (Morgan, 1991). *E. underwoodi* is primarily a tropical bat and is no longer found

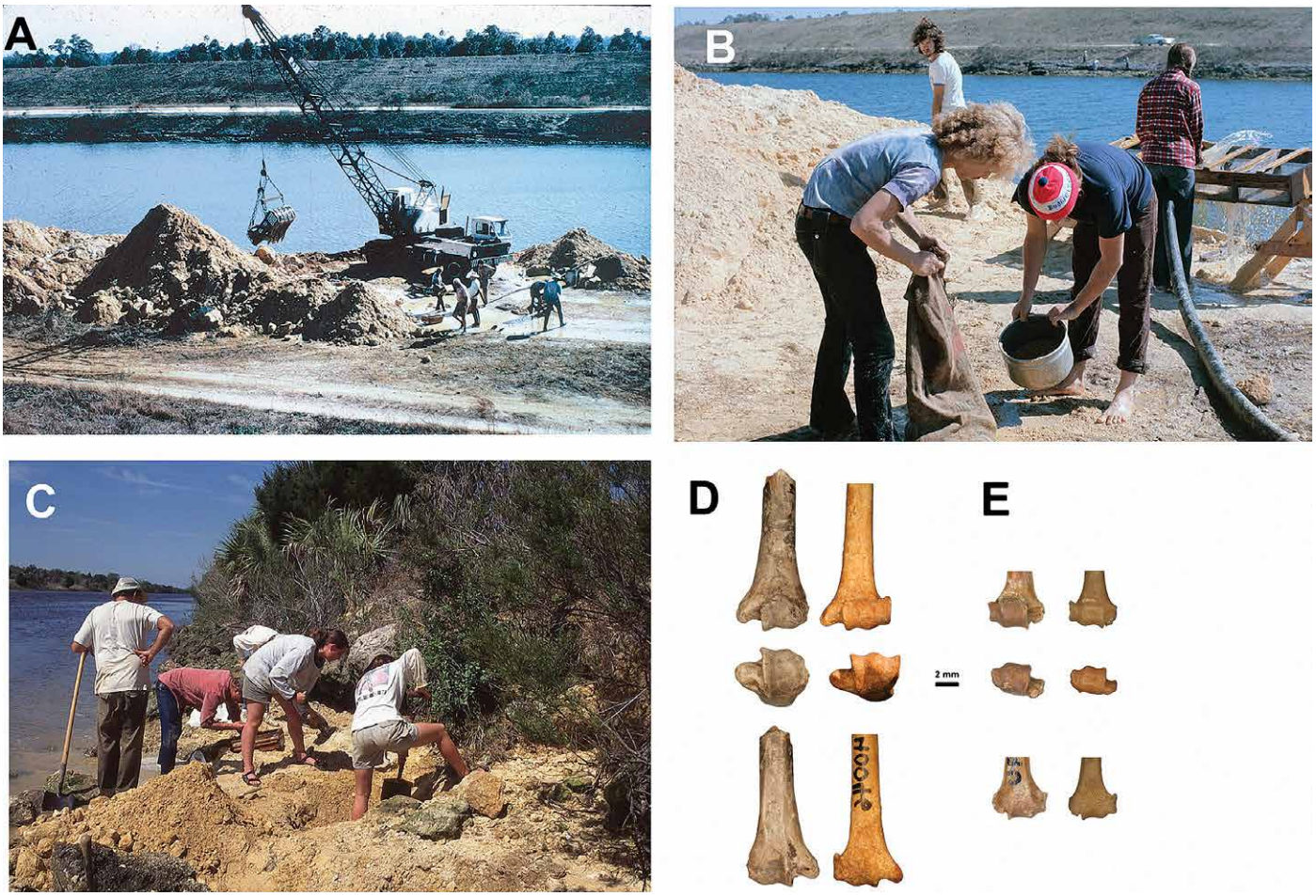

Figure 11. Inglis fossil sites, along the now-abandoned Cross-Florida Barge Canal, Citrus County, Florida, early Pleistocene (late Blancan NALMA). (A, B) Field crew working the Inglis 1A site. (A) Dragline removing in-place sediment from Inglis 1A. (B) Field crew screenwashing sediments from Inglis 1A. (C) Field crew excavating the Inglis 1C site. (Photos in A, B courtesy of David Webb; photo in C courtesy of Steven Emslie.) (D) Distal ends of the humerus of vampire bats, genus *Desmodus*, in anterior, distal, and posterior views, from top to bottom: *D. archaeodaptes*, Inglis 1A (right) and *D.* aff. *draculae*, El Breal de Orucual, late Pliocene/early Pleistocene of Venezuela (left) (Photos from Czaplewski and Rincon, 2020). (E) Distal ends of the humerus of pallid bats, genus *Antrozous*, in anterior, distal, and posterior views, from top to bottom: *Antrozous* sp. from Inglis 1A (left) and modern specimen of *A. pallidus* (right).

in Florida, now occurring from southern Arizona to Nicaragua. We hypothesize that an overland dispersal route from the southwestern United States of about 2,500 km is more likely than the somewhat shorter (~1,500 km) but overwater dispersal route across the Gulf of Mexico from southeastern Mexico or northern Central America.

Chiroptera from Early and Middle Pleistocene (Blancan and Irvingtonian) Karst Deposits in Florida

No cave deposits in Florida are older than late Pleistocene, but there are more than 25 karst-derived vertebrate faunas of early to middle Pleistocene age (Blancan and Irvingtonian NALMAs) from peninsular Florida, several of which represent former cave deposits based on the abundance of bats, as well as geologic and taphonomic features of the sites (Morgan and Hulbert, 2008), including Coleman 2A, Haile 16A, Haile 21A, and Inglis 1A (Appendix). The late Irvingtonian (~0.25–0.5 Ma) Coleman 2A LF from Sumter County in central Florida is a sinkhole deposit that produced three extant species of cave-dwelling vespertilionid bats, *Myotis austroriparius*, *Pipistrellus* (=*Perimyotis*) *subflavus*, and Rafinesque's big-eared bat, *Plecotus* (=*Corynorhinus*) *rafinesquii*, all of which still live in the Florida peninsula (Martin, 1974). Two early Pleistocene (early Irvingtonian, ~1.0–1.6 Ma) karst deposits, Haile 16A and Haile 21A, are sinkholes or fissures in the Haile Quarry complex in Alachua County, both of which produced fossils of the extinct vampire bat, *Desmodus archaeodaptes*, with Haile 21A as the type locality. This vampire is a smaller species than the late Pleistocene *D. stocki*, similar in size to the living *D. rotundus* but differing in several cranial characters (Morgan et al., 1988). Haile 16A and Haile 21A also produced large samples of *M. austroriparius*, indicating these two karst deposits originally formed as caves.

The most diverse NA chiropteran fauna of early Pleistocene age (late Blancan) is from Inglis 1A, a karst deposit located along the now-abandoned Cross-Florida Barge Canal in Citrus County, about 10 km inland from the Florida Gulf Coast. The site consisted of layers of sand and clay filling a large solution cavity in limestone of the marine Eocene

Inglis Formation. Figures 11A–C show field crews excavating and screenwashing the Inglis 1A site and the nearby Inglis 1C site of similar age and origin (Ruez, 2002). Inglis 1A documents the earliest known occurrence of the vampire bat, *Desmodus archaeodaptes* (Fig. 11D), together with six genera of vespertilionid bats, *Antrozous* (Fig. 11E), *Corynorhinus*, *Eptesicus*, *Lasiurus*, *Myotis*, and *Perimyotis* (Morgan, 1991). The abundance of cave-dwelling bats, in particular species of *Corynorhinus*, *Myotis*, and *Perimyotis*, indicates the Inglis 1A site was a part of an extensive cave system in the early Pleistocene. Inglis 1A documents the only Blancan record of the big-eared bat genus *Corynorhinus* and one of only two Blancan sites with *Perimyotis*. The Inglis 1A record of *Antrozous* represents the first occurrence of this genus in eastern North America. The closest modern record of the pallid bat, *Antrozous pallidus*, is in central Texas more than 1,500 km west of the Florida peninsula, although a related subspecies or species, *Antrozous pallidus koopmani* or *A. koopmani*, occurs in Cuba (Silva Taboada, 1976, 1979; Silva and Vela, 2009; García and Mancina, 2011; Orihuela et al., 2020a, b). Morgan and Emslie (2010) documented a number of extralimital mammals and birds from Inglis 1A that had western affinities, including *Antrozous* and the jackrabbit, *Lepus*.

The late Blancan Inglis 1A and early Irvingtonian Haile 16A sites are notable for their diverse faunas of large mammals of South American origin that participated in the Great American Biotic Interchange (GABI), including (Webb, 1976; McDonald, 2005; Morgan, 2005): three genera of ground sloths, *Eremotherium*, *Megalonyx*, and *Paramylodon*; the pampathere or giant armadillo, *Holmesina*; and a large, extinct species of the extant armadillo genus *Dasypus*. Additional GABI species from these two faunas include: the giant, flightless predatory bird, *Titanis*, a member of the otherwise endemic South American family Phorusrhacidae; the large glyptodont, *Glyptotherium*; and the capybara, *Neochoerus*, in Inglis 1A and the smaller glyptataeline glyptodont, *Pachyarmatherium*, in Haile 16A. Morgan (1991) hypothesized that *Desmodus*, a phyllostomid bat of South American origin, dispersed into NA as a participant in the GABI after the connection of North and South America at the Panamanian Isthmus at about 5 Ma, arriving in Florida in the early Pleistocene (~ 2 Ma) at Inglis 1A, following its favored prey species, probably ground sloths or other large xenarthrans, northward.

Chiroptera from Oligocene and Miocene Karst Deposits in Florida

North American fossil deposits of karst origin that contain bats of Miocene and Oligocene age are known almost exclusively from peninsular Florida (Czaplewski et al., 2008; Morgan and Czaplewski, 2012, 2023). The taphonomy of these karst deposits, which include sinkhole fills, fissure deposits, and isolated sediment pockets in solution cavities, as well as the frequent presence of bat fossils, indicates their prior existence as caves. Florida early Miocene and Oligocene (~18–30 Ma) karst deposits provide important data pertaining to the mid Cenozoic chiropteran fauna of southeastern NA, including the earliest New World representatives of several families of Neotropical bats: sac-winged bats (Emballonuridae), ghost-faced and mustached bats (Mormoopidae), and funnel-eared bats (Natalidae), as well as the extinct family Speonycteridae. All of these bats indicate a warmer tropical to subtropical climate in Florida during the Oligocene and early Miocene. The oldest cave-dwelling bats in NA (~26–30 Ma) were also members of these same four families. The richest pre-Pleistocene bat faunas from Florida are from three karst sites, the early Oligocene I-75, late Oligocene Brooksville 2, and early Miocene Thomas Farm (Czaplewski et al., 2003b; Morgan and Czaplewski, 2003, 2012, 2023; Czaplewski and Morgan, 2012; Morgan et al., 2019). These sites are discussed here from oldest to youngest.

The I-75 site was discovered in a roadcut on Interstate Highway 75 (I-75) in Gainesville, Alachua County, northern peninsular Florida, and was destroyed by road-building activities shortly thereafter. The fossiliferous sediments in the I-75 site consisted of massive, dark, silty clays, deposited in a small karst solution feature 5 m in diameter and 2 m deep, developed in marine Eocene limestone. Considering the small size of the fossiliferous deposit, the I-75 site has a diverse vertebrate fauna composed of about 35 terrestrial and freshwater species: toads, salamanders, turtles, lizards, snakes, and about 20 species of mammals, including seven species of bats (Patton, 1969; Hayes, 2000; Czaplewski and Morgan, 2012; Morgan and Czaplewski, 2012, 2023; Morgan et al., 2019). Mammalian biochronology confirms that I-75 is the oldest land vertebrate fauna known from Florida, dating to the early Oligocene (late Whitneyan NALMA; 30–31 Ma; Patton, 1969; Prothero and Emry, 2004; Morgan and Czaplewski, 2023). Most of the bats from I-75 belong to families now found in the New World tropics but no longer occur in Florida, including: an extinct genus and two new species of Emballonuridae, *Oligopteryx floridanus* and *O. hamaxitos*, representing the earliest known Neotropical members of the family (Morgan and Czaplewski, 2023); an extinct genus and species, *Koopmanycteris palaeomormoops*, of Mormoopidae, the oldest known member of this family (Morgan et al., 2019); and an indeterminate genus and species representing the earliest record of the family Natalidae (Morgan and Czaplewski, 2003). An extinct genus and two new species identified from I-75, *Speonycteris aurantiadens* and *S. naturalis*, belong to the extinct family Speonycteridae that also has Neotropical affinities and, together with the mormoopid, *Koopmanycteris*, are the oldest known members of the superfamily Noctilionoidea (Czaplewski and Morgan, 2012). The abundance of bats in the I-75 LF, in particular, the Mormoopidae, which are primarily obligate cave-dwelling species (Smith, 1972), the abundance of other small terrestrial vertebrates, and the karst structure of the fossil deposit, all strongly indicate this site originally formed in a cave.

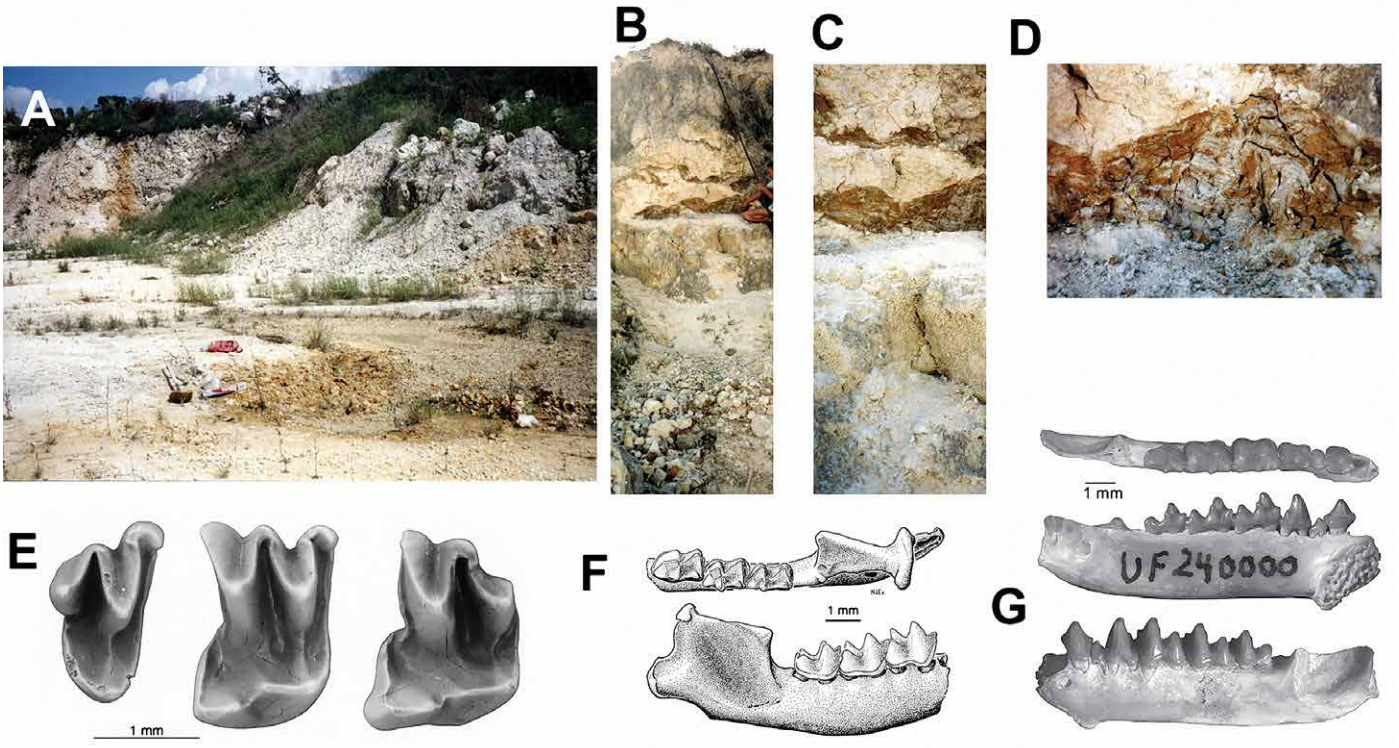

Figure 12. Brooksville 2 Quarry, Hernando County, Florida. (A) Overview of the Brookville 2 Quarry. (B–D) Series of three photos showing the same fissure deposit in the Brooksville Quarry, with each photo a closer view (from left to right). (Photos A–D courtesy of Glynn Hayes.) (E) Occlusal views of three upper molars of *Oligopteryx floridanus*, an extinct genus and species of Emballonuridae (Photos from Morgan and Czaplewski, 2023). (F) Mandible in occlusal view (top) and lateral view (bottom) of *Koopmanyteris palaeomormoops,* oldest member of the Mormoopidae (Illustrations from Morgan et al., 2019). (G) Mandible in occlusal, medial, and lateral views, from top to bottom, of *Speonycteris aurantiadens* in the extinct family Speonycteridae and oldest member of the Neotropical Noctilionoidea (Photos from Czaplewski and Morgan, 2012).

The Brooksville 2 site was discovered in a limestone quarry near Brooksville, Hernando County, central Florida (Fig. 12A). The site consists of clays and sands filling several small karst solution features or fissure deposits developed in the marine Oligocene Suwannee Limestone (Hayes, 2000; Figs. 12B-D). Although specimens of larger vertebrates were found on the surface, FLMNH field crews collected the fossils primarily by screenwashing because of the abundance of microvertebrates. The vertebrate assemblage from Brooksville 2 consists of frogs, lizards, snakes, and a diverse fauna of both large and small mammals, including five species of bats (Hayes, 2000; Czaplewski and Morgan, 2012; Morgan et al., 2019; Morgan and Czaplewski, 2023). The mammalian biochronology of the Brooksville 2 LF indicates a late Oligocene age (early Arikareean NALMA; 26-28 Ma; Hayes, 2000). Four of the five species of bats from Brooksville 2 are the same species with tropical affinities found at I-75: the emballonurids, *Oligopteryx floridanus* (Fig. 12E) and *O. hamaxitos*; the mormoopid, *Koopmanycteris palaeomormoops* (Fig. 12F); and the speonycterid, *Speonycteris aurantiadens* (Fig. 12G), all of which were described as new genera and species from Brooksville 2 (Czaplewski and Morgan, 2012; Morgan et al., 2019; Morgan and Czaplewski, 2023). As with I-75, the abundance of bats, particularly the mormoopid, *Koopmanycteris*; the abundance of small terrestrial vertebrates; and the karst origin of the solution features and sediments, all point to the Brooksville site having formed as a cave.

The Thomas Farm site near Bell in Gilchrist County, northern peninsular Florida, is the best known and most diverse early Miocene (early Hemingfordian NALMA; ~18 Ma) vertebrate fauna in eastern NA. The site consists of clays and sands filling a 30 m-deep, vertical-walled sinkhole, developed in marine Eocene limestone (Pratt, 1989, 1990; Figs. 13A-C). Thomas Farm has produced a diverse vertebrate fauna of about 90 species, with more than 20 species of large mammals and nearly 70 species of small vertebrates consisting of frogs and toads, salamanders, lizards, snakes, one of the largest Miocene avifaunas in NA, shrews, rodents, and a large sample of bats (Pratt, 1989, 1990; Czaplewski and Morgan, 2000; Morgan and Czaplewski, 2003, 2012, 2023). Many of the small vertebrates appear to have been deposited in a former cave system developed in the wall of the sinkhole (Fig. 13C), either as a coprocoenosis derived from the scat of small mammalian carnivores, the pellets of raptorial birds, or through the natural accumulation of carcasses on a cave floor in the case of the bats (Pratt, 1989). Thomas Farm has the largest bat sample from any Tertiary fossil deposit in NA, with more than 3,000 identified specimens (University of Florida/

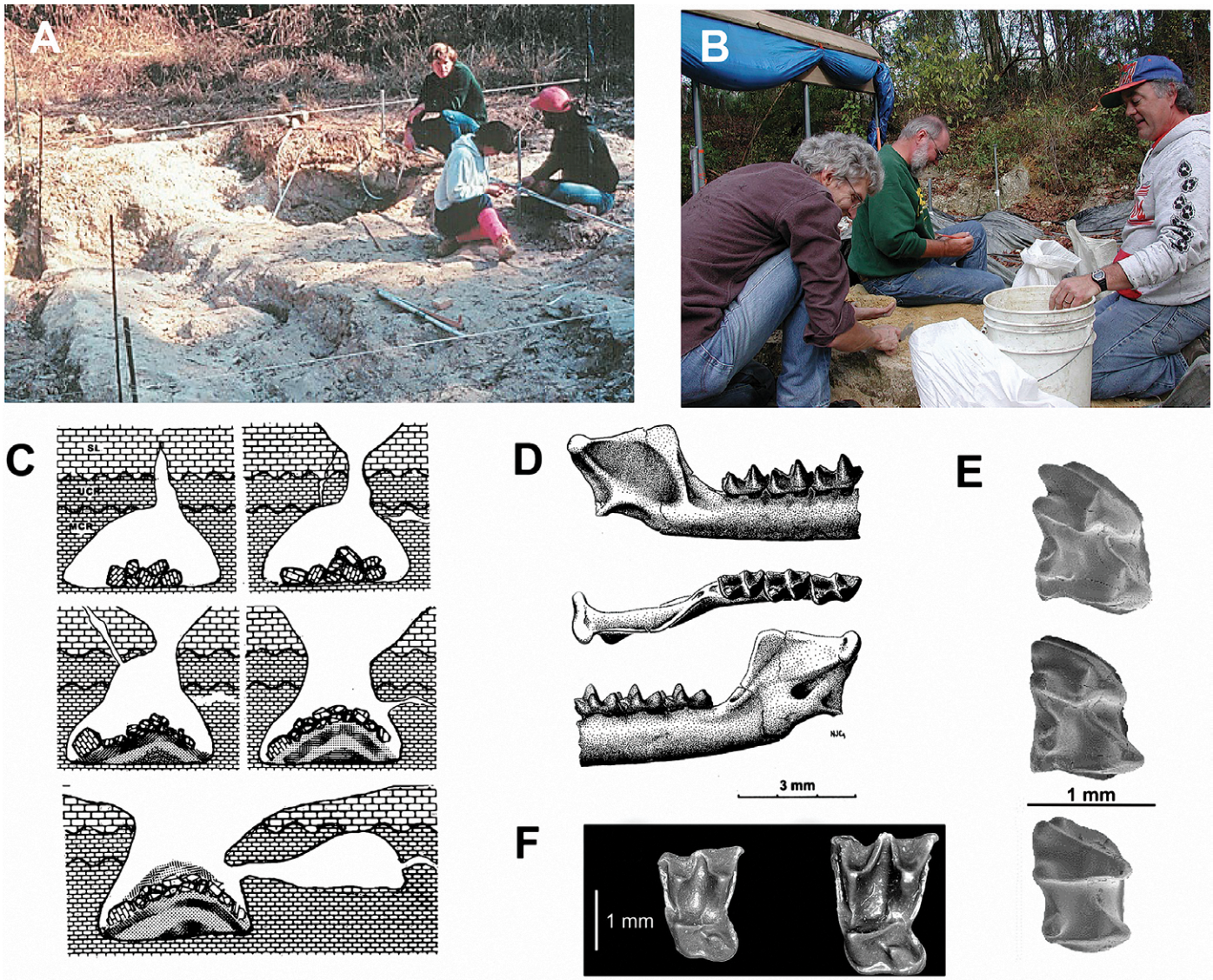

Figure 13. Thomas Farm site, a karst sinkhole-cave complex, Gilchrist County, Florida, early Miocene, (early Hemingfordian). (A) Steven Emslie (top), Ann Pratt (left), and GSM (right) excavating the Thomas Farm site (Photo courtesy of Richard Hulbert). (B) NJC (left), Arthur Poyer (center), and GSM (right) collecting sediments to screenwash for fossil bats (Photo courtesy of Erika Simons). (C) Schematic cross-sections showing how the Thomas Farm site formed as a 30 m deep sinkhole in Eocene marine limestone. Lowermost cross-section shows a cave in the wall of the sinkhole. Layers of sand and clay filled the sinkhole, including cave sediments with bat fossils (Illustrations from Pratt, 1990). (D) Type mandible of *Primonatalus prattae*, in lateral, occlusal, and medial views, from top to bottom, an extinct genus and species of bat in the endemic Neotropical family Natalidae (Illustrations from Morgan and Czaplewski, 2003). (E) Occlusal views of three lower molars of *Floridopteryx poyeri*, a new genus and species of bat in the tropical family Emballonuridae (Photos from Morgan and Czaplewski, 2023). (F) Occlusal views of upper molars of two undescribed species of Molossidae (Photos from Czaplewski et al., 2003b).

FLMNH vertebrate paleontology database) representing at least nine species. Four of the Thomas Farm bats belong to families with Neotropical affinities: an extinct genus and species of Natalidae, *Primonatalus prattae* (Morgan and Czaplewski, 2003; Fig. 13D); an extinct genus and species of Emballonuridae, *Floridopteryx poyeri* (Morgan and Czaplewski, 2023; Fig. 13E); and two undescribed species of Molossidae (Czaplewski et al., 2003b; Fig 13F). The other five species belong to the Vespertilionidae, three of which are extinct genera and species known only from Thomas Farm, *Karstala silva*, *Miomyotis floridanus*, and *Suaptenos whitei* (Lawrence, 1943; Czaplewski and Morgan, 2000). The remarkable sample of bats, in particular the natalid *Primonatalus prattae*, a member of an endemic Neotropical family (Natalidae) in which all living species are obligate cave dwellers (Morgan and Czaplewski, 2003; Tejedor, 2011), supports data from the geology, taphonomy, and remainder of the vertebrate fauna that Thomas Farm formed, at least in part, as an extensive cave system.

The I-75, Brooksville 2, and Thomas Farm sites provide important data on the deep-time evolution of the North American chiropteran fauna, including the earliest records of the taxonomic diversity and community structure of NA mid-Cenozoic bats (between 18 and 30 Ma). The Oligocene I-75 and Brooksville 2 faunas document the oldest

members of several endemic Neotropical bat families, as well as the earliest evidence of cave-dwelling bats in the New World. Although there are older bats in NA from several Eocene faunas, these fossils are from non-karst depositional environments, mostly from lacustrine or lake sediments, and thus, we are not able to determine if they may have been cave-roosting species. However, at least one Eocene species of archaic bat of indeterminate family, *Vielasia sigei,* has been found abundantly preserved in cave sediments in a locality in France, indicating that some bats had already adopted caves by about 50 Ma (Hand et al., 2023), and other bat fossils are widely known from Eocene karstic deposits elsewhere in Europe as well as in Africa and Asia (e.g., Sigé & Legendre, 1983; Maitre, 2014; Ravel et al., 2013, 2016). The Florida Oligocene (~26-30 Ma) chiropteran faunas from I-75 and Brooksville 2 are composed almost exclusively of species with tropical affinities (Emballonuridae, Mormoopidae, and Speonycteridae), whereas the early Miocene (~18 Ma) bat fauna from Thomas Farm is 10 million years younger and about evenly divided between species with tropical (Emballonuridae, Natalidae, Molossidae) and temperate (Vespertilionidae) affinities. The transition from a mostly tropical chiropteran fauna in Florida in the Oligocene to a combination of tropical and temperate species in the early Miocene, was followed by the disappearance of tropical bats in Florida by the middle Miocene. (Morgan and Czaplewski, 2023). As noted above, a few extralimital species of bats with tropical affinities are recorded from Florida late Pleistocene faunas.

There is a long gap in the fossil record of bats in Florida after the Thomas Farm site, extending from the early Miocene to the end of the Pliocene (~18–2.6 Ma), during which there are no sites of karst origin that contain extensive chiropteran faunas, suggesting a lack of former cave deposits during this time interval. The sparse sample of bats from Florida middle Miocene through Pliocene sites consists entirely of vespertilionids (Morgan and Czaplewski, 2012). There are numerous vertebrate faunas of karst origin in northern peninsular Florida during this time period, particularly the late Miocene (Clarendonian and Hemphillian NALMAs; ~7–10 Ma), including: Love Bone Bed, McGehee Farm, Haile 19A, Mixson's Bone Bed, Tyner Farm, and Withlacoochee River 4A. These sites formed in a limestone karst terrain but not in caves, including sinkhole ponds, nearshore marine or estuarine lagoonal or deltaic deposits, fluvial deposits, natural traps, or other taphonomic settings that contained few or no bats (Morgan and Hulbert, 2008). The geologic explanations for the lack of karst deposits of cave origin in Florida from the middle Miocene through the late Pliocene are varied but would have included high water tables during periods of high sea level that would have flooded caves, periods of even higher sea level that would have completely submerged the Florida peninsula, and the deposition of a thick overburden of clastic sediments (clays and sands) overlying the Paleogene carbonate bedrock that would have impeded cave and karst development.

FUTURE DIRECTION OF RESEARCH ON NORTH AMERICAN FOSSIL BATS

Late Pleistocene cave deposits containing bats and other vertebrate fossils are common throughout North America, as reviewed above, and additional fossiliferous caves continue to be found as cavers and cave paleontologists explore caves throughout the continent. Early to middle Pleistocene (Irvingtonian) cave deposits are much less common in NA, and very few sites of this age with significant bat samples have been discovered over the past several decades. Prior to the early Pleistocene (early Irvingtonian; ~1 Ma), cave deposits with Tertiary vertebrate fossils are unknown anywhere in NA and fossiliferous karst deposits are rare, except in Florida. Unlike the Pleistocene record, most Tertiary fossil sites from NA containing bats, once again exclusive of Florida, occur in open or non-karst depositional settings, including paleosol, alluvial, fluvial, or lacustrine deposits, and mainly consist of small samples of fragmentary specimens, rather than larger samples of better-preserved bat fossils typical of caves and karst depositional environments (Czaplewski et al., 2008). An exception is the earliest known bats from NA that consist of several remarkably complete skeletons from early Eocene (~50-52 Ma) lake deposits in the Green River Formation of Wyoming (Jepsen, 1966; Simmons et al., 2008; Rietbergen et al., 2023). Fossil bats occur sporadically in western NA in the Eocene, Oligocene, Miocene, and Pliocene, almost all of which are from non-karst deposits (Czaplewski et al., 2008). Bats older than late Pleistocene are unknown from the West Indies, and only a few pre-late Pleistocene records of bats are known from Mesoamerica, none of which are from cave or karst deposits.

As we have documented for Florida, former caves now preserved as various types of karst features, such as sinkholes, fissures, or solution cavities, often preserve sediments that contain fossils of bats. Because of an abundance of fossil-bearing karst deposits, ranging in age from early Oligocene to late Pleistocene, Florida has the richest fossil chiropteran record in North America (Czaplewski et al., 2008; Morgan and Hulbert, 2008). However, for reasons still unclear to us, similar karst deposits containing vertebrate fossils are rare or absent elsewhere in NA, particularly during the Tertiary. Conard Fissure in Arkansas is a notable middle Pleistocene (Irvingtonian) karst fissure deposit containing an abundant bat fauna (Brown, 1908). As described by Winkler and Gose (2003), the early Pleistocene (early/medial Irvingtonian) Fyllan Cave site in Texas consists of sediments preserved in a small solution cavity representing a former cave developed in Cretaceous limestone in an abandoned quarry. Prior to the Irvingtonian, there are only a handful of early Quaternary and Tertiary karst deposits in NA, outside of Florida, that contain vertebrate fossils and even fewer

that contain bats. Considering the widespread occurrence of potential karst areas throughout the US (Fig. 1), the paucity of Tertiary karst deposits containing vertebrate fossils in puzzling, especially taking into account the widespread occurrence throughout southern Europe of Tertiary karst sites containing bats (Sigé and Legendre, 1983; Gunnell and Simmons, 2005).

It is also worth noting that pre-late Pleistocene cave and karst deposits containing bats are unknown from South America, which is a major contributing factor to the poor Tertiary chiropteran record on that continent (Morgan and Czaplewski, 2012, 2023). However, the potential for such sites in South America has been hinted at by previous researchers (Hartenberger et al., 1984). The famous fossiliferous beds of late Paleocene age at low elevation near the Brazilian coast at Itaboraí have such potential and have produced diverse notometatherians and eutherians, including microvertebrates (Bergqvist et al., 2008), but are apparently too old to preserve bats. No large-scale historical geological settings and situations similar to the bat-rich Florida peninsula or Quercy phosphorites and other fissure fillings in Europe are known in South America, but perhaps small areas of karstified limestone similar to those of the continental interior (such as NA sites mentioned below) could occur along the Andean cordillera where the limestones have been uplifted and abut Paleogene or Neogene sedimentary rocks? Perhaps searching by remote sensing such as the approach explored by Anemone et al. (2011a, 2011b) and Emerson and Anemone (2012) would help?

The distribution of karst terrain across the Earth's continents is uneven (Williams and Ford, 2006) and could partly explain the presence or absence of cave- or karst-related bat fossils in each. Although we have not systematically or even cursorily examined these deposits or why they bear or lack vertebrate fossils including bats, we mention a few of the more notable Tertiary karst deposits on other continents that have produced important samples of fossil bats. The rich record from southern Europe is mentioned above. The famous Riversleigh World Heritage Area in Australia consists of an extensive region of limestone with karst deposits that holds a treasure-trove of Oligocene and Miocene vertebrate fossils including a high diversity of fossil bats (e.g., Hand and Kirsch, 2003; Hand et al., 2005, and references therein). Less well searched but fossiliferous karstic rocks and formations of Cenozoic age also occur in many parts of Africa including the circum-Mediterranean region, like those in southern Europe (Gunnell et al., 2016). Fossil bats are known from Neogene deposits in Angola, Botswana, and Namibia in southwestern Africa, with the most notable being the Otavi Mountain karst in Namibia that has produced large and diverse samples of Miocene bats (e.g., Pickford et al., 1994; Rosina and Pickford, 2019). Karst deposits in Asia have also produced fossil bats (e.g., Ravel et al., 2013).

We briefly mention two late Pliocene or early Pleistocene (Blancan) karst deposits containing vertebrate fossils in western North America. The Blancan Anita LF was derived from a karst fissure deposit in the Permian Kaibab Limestone in the Val Verde Copper Mine, Coconino County, northern Arizona (Hay, 1921). The Anita fauna was collected in the early 1900s, long before the advent of screenwashing, so very small vertebrates, such as bats and shrews, are absent from the fauna. However, the abundance of rabbits from Anita (Hay, 1921; GSM, personal observation), as well as the occurrence of three species of medium-sized rodents, two sciurids, and the woodrat, *Neotoma*, suggests that smaller mammals, including bats, were probably present in the Anita fissure deposit but were not collected. Unfortunately, the Anita site no longer exists. The Richmond Hill fissure deposits, from a gold mining region in the northern Black Hills, Lawrence County, southwestern South Dakota, have produced a Blancan mammal fauna, including small vertebrates (Guthrie, 2005; J. Mead and N. Fox, personal communication). Jim Mead, Chris Jass, and Nate Fox are planning further work on the small vertebrate fauna from the Richmond Hill fissure deposits (see Mead et al., this volume). We are hopeful these sites may eventually produce Pliocene or early Pleistocene (Blancan) bats.

Within the past few decades, two latest Miocene or earliest Pliocene (latest Hemphillian NALMA) karst deposits have been discovered in the continental interior of eastern North America, the Gray Fossil Site in Tennessee and the Pipe Creek Sinkhole in Indiana. These two sites were discovered in the same way most Florida karst sites were first found, by excavation with heavy equipment. The Gray Fossil Site was uncovered during the construction of a road and the Pipe Creek Sinkhole was found in a commercial mining operation. Since their initial discovery, both sites have been carefully excavated by paleontologists and both contain diverse samples of small mammals and other small vertebrates collected by screenwashing. The Gray Fossil Site is a sinkhole pond or lake that formed in the Appalachian Valley and Ridge karst region composed of Paleozoic carbonate rocks. The Gray Fossil Site has produced a diverse latest Hemphillian vertebrate fauna (Wallace and Wang, 2004; Hulbert et al., 2009), including two species of vespertilionid bats: one tentatively referred to the living species, *Eptesicus fuscus*, one of the most common and widespread bats in NA, and a second smaller bat indeterminate at the genus and species levels (Czaplewski, 2017). Excavation and screenwashing for microvertebrates are ongoing at the Gray Fossil Site, so there is the potential for the recovery of additional bat specimens.

The Pipe Creek Sinkhole in Indiana is a sinkhole developed in a Silurian reef deposit in which a cave formed and then collapsed, eventually resulting in a sinkhole pond containing both freshwater and terrestrial vertebrates (Farlow et al., 2001). The Pipe Creek Sinkhole contains abundant microvertebrates, including a diverse rodent fauna with small cricetids and one species of each of rabbit and shrew (Farlow et al., 2001; Martin et al., 2002; Czaplewski et al., 2012).

Unfortunately, the Pipe Creek Sinkhole deposit appears to have been mined out and did not yield any bat fossils (J. O. Farlow, personal communication). We are not aware of any NA Eocene, Oligocene, or early- to middle-Miocene karst sites with vertebrate fossils, outside of Florida, although the NA Tertiary record of karst fossil deposits is surely incomplete.

In comparison with the remainder of the North American continent, which has fewer than 10 Tertiary karst deposits containing vertebrate fossils, the Florida peninsula has more than 30 vertebrate-fossil-bearing paleokarst deposits of Oligocene and Miocene age (none are known from the Pliocene) and another 20 sites of early Pleistocene age (late Blancan and early Irvingtonian) (Morgan and Hulbert, 2008). The geologic circumstances that have led to the development of an extensive karst terrain in Florida are discussed above and have resulted in an abundance of both dry and submerged caves, springs, and various types of paleokarst deposits such as sinkholes, solution cavities, and fissures (Lane, 1986; Florea, 2008; Fig. 9). Factors that have resulted in the discovery of large numbers of paleokarst fossil sites in Florida include: extensive commercial limestone mining operations in northern peninsular Florida, regular surveys of these mines by paleontologists from the FLMNH, a large contingent of avocational paleontologists who are continually scouring the Florida landscape in search of new fossil sites, the popularity of scuba diving in Florida rivers and springs, and a dedicated cadre of experienced cave divers.

A major underexploited source of fossil bats in NA is from underwater caves, which are numerous in Florida, the Yucatán Peninsula of Mexico, Belize, and Guatemala, and on islands throughout the Greater Antilles and Bahamas. Dan's Cave, Ralph's Cave, and Sawmill Sink on Abaco in the Bahamas (Fig. 7) and Oleg's Bat Cave in the Dominican Republic (Fig. 8) demonstrate the tremendous potential of underwater caves to produce large and well-preserved samples of fossil bats and other vertebrates (Steadman et al., 2007; Velazco et al., 2013; Soto-Centeno and Steadman, 2015). Other islands in the Bahamas, including Acklins, Andros, Eleuthera, Grand Bahama, and Mayaguana, contain underwater caves or blue holes that have produced fossils of extinct or extirpated tortoises, crocodiles, and rodents, and could potentially yield fossil bats (Morgan and Albury, 2013). We know from discussions with cave divers that underwater caves exist on other West Indian islands (e.g., Cuba, Puerto Rico, and Grand Cayman), but these caves have not been systematically explored for fossils. Several underwater caves or cenotes in the Yucatán Peninsula of Mexico have produced well-preserved samples of large mammals of late Pleistocene age, including ground sloths and carnivores from Hoyo Negro in the state of Quintana Roo (McDonald et al., 2017; Schubert et al., 2019), as well as bats (Cruz et al., 2024).

Late Pleistocene vertebrate fossils have been known from underwater caves and springs of karst origin in Florida since the 1930s, following the discovery of a skeleton of the American mastodon, *Mammut americanum*, in Wakulla Springs in the Florida Panhandle south of Tallahassee by Herman Gunter of the Florida Geological Survey. Beginning in the 1950s and 1960s, with the early development and refinement of scuba diving techniques, and continuing to the present, paleontologists from the FLMNH have worked with a large contingent of scuba divers to systematically survey the rivers, springs, sinkholes, and underwater caves of peninsular Florida for vertebrate fossils (Webb, 1974). Many rivers in Florida, including the Aucilla River, Ichetucknee River, Ocklawaha River, Peace River, Santa Fe River, St. Johns River, and Waccasassa River, among others, have produced large samples of late Pleistocene vertebrate fossils, some of which are derived from what are now underwater caves or karst deposits. However, for various reasons, including the difficulty in collecting fossils underwater using scuba gear, most of the fossil samples from Florida rivers consist of large mammals and other large vertebrates, with only limited samples of small vertebrates and few bats. Many Florida underwater sites in rivers and springs are either not of karst origin, or if karst in origin (e.g., sinkhole ponds/lakes), do not represent former dry caves and would not be expected to contain fossil bats.

Only three underwater fossil sites in Florida have been systematically collected for smaller vertebrates. The late Pleistocene (Rancholabrean) Page-Ladson site in the Aucilla River in the eastern Florida Panhandle produced a diverse sample of fish, amphibians, reptiles, birds, and small mammals, but no small rodents, shrews, moles, or bats (Webb and Simons, 2006). The absence of small vertebrates in the Page-Ladson fauna was almost certainly a result of the collecting technique in which unconsolidated sediments were "vacuumed" from the bottom of the Aucilla River using a dredge and then washed though a ¼-inch screen. Mammals in the size category of rabbits, squirrels, muskrats, and porcupines were collected using this technique (Webb and Simons, 2006), but few vertebrates smaller than ¼ inch, such as frogs, lizards, passerine birds, cricetid rodents, and bats, were recovered. Moreover, the late Pleistocene depositional setting of the Page-Ladson site in the Aucilla River was a sinkhole pond, which was probably not conducive to the preservation of bat fossils (Webb and Simons, 2006). The two Florida late Pleistocene underwater sites that have produced bats, Devil's Den and Rock Springs, are both underwater caves, not river deposits, as described in more detail above.

Most of the fossiliferous karst deposits in Florida have been discovered during commercial mining operations, as was three of the four Tertiary fossil sites from elsewhere in the US. The Pliocene Anita Fauna in Arizona was found in a fissure deposit in a copper mine, the Pliocene Richmond Hill fissure deposits in South Dakota occur in a gold

mining region, and the latest Miocene/earliest Pliocene Pipe Creek Sinkhole is a sinkhole representing a former cave uncovered during limestone mining operations. Other karst sites have been uncovered during road building operations, including the latest Miocene/earliest Pliocene Gray Fossil Site in Tennessee and the early Oligocene I-75 Fauna in Florida, named for Interstate Highway 75 whose construction near Gainesville, Florida, led to the discovery of this site. Initial excavations for the now-abandoned Cross-Florida Barge Canal in the 1960s led to the discovery of 15 early Pleistocene (Blancan) karst sites near Inglis, just inland from the Florida Gulf Coast, Inglis sites 1A-1L and 2A-2C, all of which consist of sinkholes or fissure deposits developed in the marine Eocene Inglis Formation (Fig. 11). Other Florida Tertiary karst sites were uncovered during farming activities, including the Miocene Thomas Farm, McGehee Farm, and Tyner Farm.

However, not all early Pleistocene and Tertiary karst fossil deposits in Florida have been discovered essentially at random through mining, construction, or farming activities. A number of Florida karst sites were discovered during a systematic paleontological survey of Florida rivers by FLMNH paleontologists using scuba (Webb, 1974), including the late Oligocene Cow House Slough, late Miocene Withlacoochee River 4A, and several early Pleistocene sites in the Santa Fe River (Santa Fe River 1, 1B, 4, 8, 8A, 8C). Several important Florida karst deposits were discovered by avocational paleontologists who were scuba diving in search of fossils in Florida rivers, including the early Miocene Miller site, which has a small sample of bats in the families Molossidae and Vespertilionidae (Andreas Kerner, personal communication), and the early Pleistocene Waccasassa River 9A and Withlacoochee River 1A sites (Hulbert, 2010). Although these various types of karst sites are located in Florida, most of these field methods could be used to discover karst sites in other places in NA, particularly in areas with suitable karst geology (Figs.1A, B).

FINAL COMMENTS

We would like to make a plea to cavers, cave paleontologists, cave geologists, cave conservationists, scuba divers, and avocational paleontologists to help discover new cave and karst fossil sites in North America. A nationwide network of dedicated cavers, particularly groups associated with the National Speleological Society, find new cave fossil deposits on a regular basis. However, most of these sites occur in caves and the fossil deposits are late Pleistocene in age, improving the already robust record of NA late Pleistocene cave faunas. Older pre-Pleistocene cave and karst sites are of particular interest to our research because they may contain bat faunas composed of new genera or species that would help us better understand the earlier evolution of the NA chiropteran fauna, particularly cave-dwelling species. These older bat faunas may also be found in caves, but often occur in karst features representing former caves that are not found in a current cave environment. Examples of older pre-late Pleistocene fossil deposits in caves often consist of indurated breccias or other types of consolidated sediments that occur in the ceiling or in fissures in the walls of caves, not in unconsolidated sediments on the cave floor. Examples of older cave deposits are found in Jamaica where fossils of the large extinct rodent, *Clidomys*, were recovered from indurated breccias preserved in the ceiling of several caves, including Slue's Cave near Lluidas Vale in the Worthy Park area (Morgan and Wilkins, 2003). Uranium-series dates ranging from 100–200 ka on flowstones associated with indurated breccia deposits containing *Clidomys* fossils in two other Jamaican caves, Worthy Park Cave and Wallingford Roadside Cave, document among the oldest dated cave deposits in the West Indies (MacPhee et al., 1989; McFarlane et al., 1998). Fossils of *Clidomys* do not occur in younger Late Quaternary sediments on the floor of Jamaican caves, indicating the older breccia deposits sample a fauna that became extinct before the end of the Pleistocene. Even older cave breccias from the island of St. Barthélemy in the northern Lesser Antilles have yielded fossils of the extinct giant caviomorph rodent, *Amblyrhiza inundata*, with bracketing uranium-thorium dates providing an age of ~500 ka for these specimens (McFarlane et al., 2014). Similar breccia deposits older than late Pleistocene surficial sediments occur in caves elsewhere in the West Indies and probably the US as well.

Karst deposits of Pliocene age and older are more difficult to locate because they are usually found outside of caves, occurring in a variety of different geologic features in areas with karst geology (Figs. 1A, B). The Gray Fossil Site in Tennessee is a good example of a rich fossil deposit occurring in an area typified by karst geology. It is very likely that other buried sinkhole pond or lake deposits, and probably fissure deposits as well, occur in this vast region of karst geology extending from Pennsylvania, Maryland, and West Virginia, south through Virginia and Tennessee to northern Georgia and Alabama. This same region is well known for caves containing late Pleistocene fossil deposits (see above), and we suspect that, as in Florida, older caves containing vertebrate fossils of Tertiary age probably existed in the Appalachians but have since collapsed through erosional processes. It is likely that mining, road building, and other construction activities in the Appalachian region will lead to more opportunistic discoveries of Tertiary fossil sites of karst origin, similar to the Gray Fossil Site. These same factors also apply to other major karst regions in the US with caves that have produced late Pleistocene cave faunas, including western Kentucky and Tennessee; the Ozark region of Arkansas, Missouri, and Oklahoma; and the Edwards Plateau of central Texas. We suspect these other regions in the US may eventually produce older, karst-derived Tertiary fossil sites containing bats. In the tropical regions of NA,

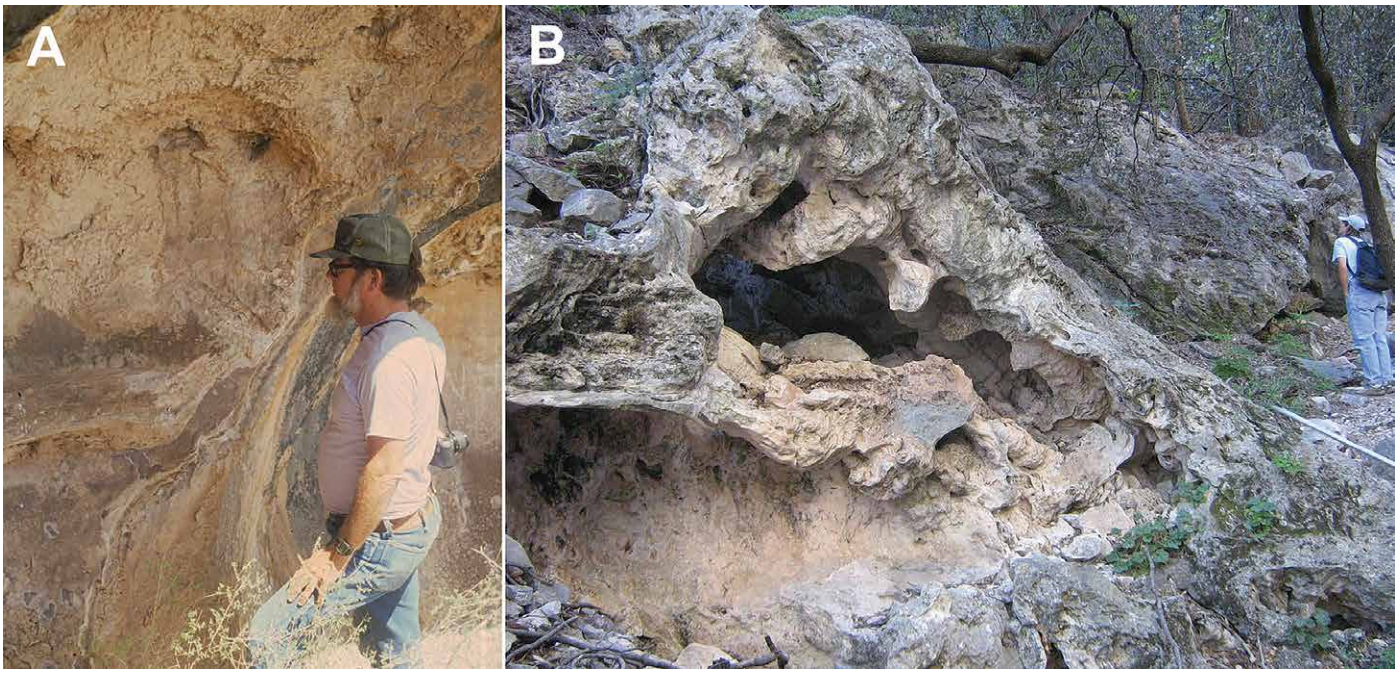

Figure 14. Paleocave remnants in southern Arizona. (A) Geologist and caver Bill Peachey in front of an ancient cave now open to the surface, showing stratified deposits (at left) reflecting former pools that could potentially yield bat fossils, Rincon Mountains. (B) Part of a former cave of unknown age, now exposed to the surface, Scheelite Canyon Trail, Huachuca Mountains.

extensive karst regions with caves exist in the Yucatán Peninsula of Mexico, Belize, and Guatemala, and throughout the larger islands in the West Indies. Late Quaternary cave faunas are common in these regions that could potentially produce older pre-late Pleistocene cave faunas, such as those mentioned above from Jamaica and St. Barthélemy, as well as older Tertiary vertebrate faunas from various types of karst features.

We mention several examples of North American karst deposits in which we regard the occurrence of vertebrate fossils as a definite possibility, even though fossils have yet to be found in these deposits. Polyak et al. (1998, 2006b) reported the occurrence of sulfate minerals, including alunite, in several caves in Carlsbad Caverns National Park (CAVE) that were produced from sulfuric acid speleogenesis. This is the process that formed the large caves in CAVE, including Carlsbad Cavern and Lechuguilla Cave, rather than the more common carbonic acid cave-forming process. $^{40}Ar/^{39}Ar$ dates on alunite deposits in caves in CAVE range in age from about 4 to 12 Ma, indicating these caves formed sometime between the early Pliocene and the middle Miocene (Polyak et al., 1996, 2006b). All vertebrate fossils currently known from CAVE are Pleistocene in age (Kottkamp et al., 2022), with the oldest fossils being middle Pleistocene (medial/late Irvingtonian, ~0.5 Ma) from Slaughter Canyon Cave. However, based on the ages indicated by these mineral deposits, considerably older sediments of Pliocene or Miocene age containing vertebrate fossils may eventually be found in CAVE.

Photos in Figure 14 show examples of former caves, now exposed at the surface, in southern Arizona. Sites like these could potentially hold ancient deposits with bats or other fossils. Figure 14A is a photo of geologist and caver Bill Peachey in front of a former cave of unknown age in the Rincon Mountains of southern Arizona now represented by a karst feature open to the surface, showing stratified deposits reflecting former pools. Interestingly, Peachey and NJC found evidence of modern bat use of this overhang as a night roost, consisting of guano and bits of stamen filaments and anthers from flowers visited by local Mexican long-tongued bats, *Choeronycteris mexicana*. Figure 14B shows a small, shelf-like stratified carbonate deposit in the Huachuca Mountains, also in southern Arizona, that were not searched, but many modern caves occur in the same mountain range and from this paleocave remnant we infer the possibility of others there. Karst deposits such as these sites in southern Arizona that represent former caves could potentially yield bat fossils, as have Tertiary karst deposits in Florida. The key is learning to recognize the various types of karst deposits, including geographic regions where they would be most likely to occur (See Fig. 1), and then surveying these areas in search of vertebrate fossil deposits.

Conservation Paleobiology and the North American Fossil Record of Bats

In closing, we note the emergence of the field of conservation paleobiology and the potential ability of bat fossils to demonstrate relatively deep-time presence of extant species and changes in evolving species, biodiversity, species distributions, and faunal composition through time and space. The fossil record of bats in caves can have important

conservation implications. A simple record of a species in a cave can show its long-term usage (for perhaps tens of thousands of years if in a stratigraphic sequence, or at least once since the Pleistocene) of the cave, justifying the preservation of the cave as a means to conserve the bat species. Theoretical biogeographic work (e.g., McGuire and Davis, 2014; Dietl et al., 2015; Jablonski and Shubin, 2015; Kemp and Hadly, 2016) can use ecological niche modeling, temporal range shifts, community- or species-level distribution changes, or paleoclimatic data to predict future pressures on a species or cave locality due to climatic changes during the Quaternary existence of a cave to inform cave management that might benefit the species inhabiting the cave. New discoveries of fossil bats may potentially add important information to these emerging fields of paleontological study.

Shelter is one of the most important resources for the survival of most animal species. Caves and rock crevices are but one type of diurnal roosting resources for bats (as well as tree bark, foliage, tree hollows, and other types of roosts [Kunz, 1982; Voss et al., 2016]). Nevertheless, these types of shelters are one of the most important for western hemisphere temperate zone bats, primarily in the families Vespertilionidae and Molossidae. This dependence emphasizes the importance of preserving caves and karstic crevices as roosting habitat for extant species. Of the bat species in NA that are currently considered imperiled or vulnerable (14 of 17 in Canada; 33 of 45 in US; 49 of 142 in Mexico; O'Shea et al. 2018; NABCA 2023), at least 31 of 45 species (~69%) in the US and Canada use caves, mostly for either day-roosting, hibernation, or night-roosting (compiled from Harvey et al. 2011). Although the fossil record of bats is relatively weak, caves and karstic fissures are particularly effective at preserving fossils of bats and other vertebrates (Andrews, 1990). The fossil record in these shelters, where available, provides a deep historical perspective on cave-dependence of many bat species. Appropriately, the conservation of bats, caves, and cave fossils are parts of the National Speleological Society's ethic of conserving all cave resources (Hildreth-Werker and Werker, 2006; Toomey, 2006).

ACKNOWLEDGMENTS

We have both spent a substantial portion of our professional careers studying fossil bats from caves and karst deposits. The list of colleagues who have helped with our field work and research on caves and karst deposits through the US and West Indies is too long to credit everyone here, but we feel it is important to thank our colleagues whose help has been particularly significant. GSM wishes to thank Nancy Albury, Carol Belski, Carol Bordegaray, Sybil Burger, Patty Daw, Glenda Dawson, Steven Emslie, Ralph Eshelman, Richard Franz, Frederick Grady, Glynn Hayes, Rodney Horrocks, Richard Hulbert, Patricia Jablonsky, Brian Kakuk, Margaret Langworthy, Gregory McDonald, Rachel Montenegro, Lannois Neely, Dale Pate, Art Poyer, Ann Pratt, Dave Steadman, Barbara and Reed Toomey, and Rickard Toomey, III. NJC would like to thank several of the same people, as well as Bill Peachey, Chris Bell, Tom Bethard, Steve Carothers, Cástor Cartelle, Cheryl and Jessica Czaplewski, Kyle Davies, Bob Emry, Jim Farlow, Francisco Goin, Richard Kay, Jen Larsen, Alvie Laverty, Ernie Lundelius, Richard Madden, Bill and Julie May, Jim Mead, Chuck Minckley, Bob and Esty Pape, Mary Poteet, Ascanio Rincon, George Ruffner, Clayton and Sylvia Russell, Marcelo Sanchez-Villagra, Blaine Schubert, Kent Smith, Steve Smith, Marcelo Tejedor, Rick Warner, Steve Willsey, and the late Bill Puckette and Sheridan Stone. For allowing us to reproduce their photographs, we thank Steven Emslie, Glynn Hayes, Rodney Horrocks, Richard Hulbert, Brian Kakuk, Phillip Lehman, and Erika Simons. In particular, Brian Kakuk and Phillip Lehman shared their spectacular photographs of bat fossils from underwater caves in Abaco in the Bahamas (BK) and the Dominican Republic (PL). Thanks to Jessica Czaplewski for help in compiling cave usage numbers. We are grateful to Jim Mead and Sharon Holte Weaver, the organizers of the symposium on cave and karst paleontology at the 2022 National Speleological Society annual meeting in Rapid City, South Dakota, and Mead and Gregory McDonald, the co-editors of this volume, for inviting us to participate in the symposium and to contribute a paper. Joaquin Arroyo-Cabrales, Chris Jass, and Jim Mead provided helpful reviews of our paper.

We dedicate this paper to the memory of our friend and colleague, Fred Grady, a talented caver and cave paleontologist who helped GSM collect and prepare large samples of bat fossils from Tobago. Fred was best known for collecting and preserving vertebrate fossils from Pleistocene cave deposits in West Virginia, including an early Pleistocene sample of the free-tailed bat, *Tadarida*, from Hamilton Cave and the northernmost fossil record of the vampire bat, *Desmodus stocki*, in eastern North America from Little Trout Cave. Fred's passing leaves a void in the field of cave paleontology that cannot be filled.

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Appendix. Species list of Cenozoic bats (Mammalia: Chiroptera) from cave and karst deposits in North America. This list is divided into the same geographic and chronologic sections as in the text. Fossil bats from caves are separated into three geographic regions: US and Canada, Mesoamerica (Mexico and Central America), and the West Indies. Fossil bats from Florida are listed separately because most of the fossil sites are karst deposits not caves. The order of families follows Simmons (2005). Within a family (subfamily for the Phyllostomidae), the genera and species are listed in alphabetical order. Extinct taxa are indicated by a dagger (†). The type locality for an extinct species is indicated by an asterisk (*). Extralimital records of a species are indicated by the pound sign (#). Quaternary records are not comprehensive; records published as "genus and species indet", "Chiroptera indet.", and "bat sp." are not included except for Oligocene-Miocene records. 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).

Age and Geography Family, genus, species	Localities[1]	Age & NALMA	References
LATE PLEISTOCENE, Canada and US except Florida			
Phyllostomidae			
Macrotus californicus.	TEXAS: Terlingua fissure filling	Late Pleistocene, Rancholabrean	Ray & Wilson, 1979; Ray et al., 1988; Simmons et al., 2020
Desmodus †*stocki*	ARIZONA: Arkenstone Cave, La Tetera Cave, Rampart Cave; CALIFORNIA: Potter Creek Cave; NEW MEXICO: U-Bar Cave; TEXAS: Sierra Diablo Cave, Terlingua fissure filling; WEST VIRGINIA: New Trout Cave	Late Pleistocene, Rancholabrean	Sinclair, 1904, 1905; Wilson, 1942; Hutchison, 1967; Ray & Wilson, 1979; Garton & Grady, 1980; Harris, 1987, 2024; Ray et al., 1988; Grady et al., 2002; Czaplewski & Peachey, 2003; Carpenter, 2004; Czaplewski et al., this volume;
Molossidae			
Eumops sp.	ARIZONA: Rampart Cave	Late Pleistocene, Rancholabrean	Carpenter, 2004
?*Nyctinomops*	NEW MEXICO: Dry Cave[2]	Late Pleistocene, Rancholabrean	Harris, 2024
Tadarida brasiliensis	ARIZONA: Bat Cave, Rampart Cave; KENTUCKY: Mammoth Cave; NEW MEXICO: Carlsbad Cavern, Dry Cave[1], U-Bar Cave; WEST VIRGINIA: Hamilton Cave; TEXAS: Hall's Cave, Lower Sloth Cave, Schulze Cave	Late Pleistocene, Rancholabrean	Dalquest et al., 1969; Harris, 1987, 2024; Grady, 1991; Toomey, 1993; Carpenter, 2004; Schubert & Mead, 2012; Moroz et al., 2021; Kottkamp et al., 2022
Vespertilionidae			
Antrozous pallidus	NEVADA: Pintwater Cave; NEW MEXICO: Conkling Cavern, Dark Canyon Cave, Dry Cave[1], Howell's Ridge Cave, Isleta Cave No. 1, Muskox Cave, Pendejo Cave, Sierra Diablo Cave, U-Bar Cave; TEXAS: Dust Cave, Upper Sloth Cave; UTAH: Crystal Ball Cave	Late Pleistocene, Rancholabrean	Sinclair, 1904, 1905; Skinner, 1942; Hutchison, 1967; Jefferson, 1982; Heaton, 1985; Harris, 1987, 2003, 2024; Emslie, 1988; Reynolds et al., 1991; Czaplewski et al., 1999; Hockett, 2000; Mead et al., 2004, 2005
Corynorhinus rafinesquii	TENNESSEE: Lookout Mountain Cave	Late Pleistocene, Rancholabrean	Gaudin et al., 2011

Corynorhinus townsendii	ARIZONA: Bida Cave, Kartchner Cavern, Papago Springs Cave, Sandblast Cave, and Skull Cave; IDAHO: Rattlesnake Cave; NEVADA: a Mormon Mountain cave; NEW MEXICO: Carlsbad Cavern, Dry Cave[1], Muskox Cave, U-Bar Cave; TEXAS: Dust Cave, Lower Sloth Cave	Late Pleistocene, Rancholabrean	Skinner, 1942; Jefferson, 1982; Harris, 1987, 2024; Emslie, 1988; Steadman et al., 1994; Czaplewski et al., 1999; NJC unpublished; Mead et al., 2005; Kottkamp et al., 2022
?*Corynorhinus townsendii*	UTAH: Crystal Ball Cave	Late Pleistocene, Rancholabrean	Heaton, 1985
Corynorhinus sp.	ILLINOIS: Meyer Cave; KENTUCKY: Mammoth Cave; MISSOURI: Crankshaft Cave; NEW MEXICO: Dry Cave[1], U-Bar Cave; PENNSYLVANIA: Frankstown Cave, Hamilton Cave; TENNESSEE: Baker Bluff Cave, Cave Without a Name, Lookout Mountain Cave; VIRGINIA: Clark's Cave; WEST VIRGINIA: New Trout Cave, Hamilton Cave	Late Pleistocene, Rancholabrean	Guilday, 1961; Parmalee, 1967; Parmalee et al., 1969; Guilday et al., 1977, 1978; Garton & Grady, 1980; Harris, 1987, 2024; Grady, 1991; Grady et al., 2002; Gaudin et al., 2011; Schubert & Mead, 2012
Eptesicus fuscus	CANADA: QUEBEC: Mine Cave, Laflèche Cave, ONTARIO: Elba Cave, Dickson Cacve, ALBERTA: Eagle Cave; US: ALABAMA: ACb-2, ACb-3, & ACb-4 Caves, Little Bear Cave; ARIZONA: Bida Cave, Pyeatt Cave, Stanton's Cave; ILLINOIS: Meyer Cave; KENTUCKY: Mammoth Cave; MISSOURI: Bat Cave, Brynjulfson Caves 1 & 2, Crankshaft Cave; NEVADA: a Mormon Mountain cave; NEW MEXICO: Carlsbad Cavern, Dry Cave[1], Howell's Ridge Cave, Muskox Cave, Sierra Diablo Cave, U-Bar Cave; OKLAHOMA: Three-Forks Cave; PENNSYLVANIA: Hamilton Cave; TENNESSEE: Baker Bluff Cave, Cave Without a Name, Lookout Mountain Cave; TEXAS: Dust Cave, Fowlkes Cave, Hall's Cave, Lower Sloth Cave, Miller's Cave, Schulze Cave, Upper Sloth Cave, Zesch Cave; VIRGINIA: Clark's Cave; WEST VIRGINIA: Hoffman School Cave, New Trout Cave	Late Pleistocene, Rancholabrean	Patton, 1963; Parmalee, 1967; Dalquest et al., 1969; Parmalee et al., 1969; Parmalee & Oesch, 1972; Hawksley et al., 1973; Guilday et al., 1977, 1978; Guilday & Hamilton, 1978; Garton & Grady, 1980; Womochel & Barnett, 1980; Jefferson, 1982; Harris, 1987, 2024; Emslie, 1988; Grady, 1991; Toomey, 1993; Grady et al., 2002; Mead et al., 2005; Sagebiel, 2010; Ebersole & Ebersole, 2011; Gaudin et al., 2011; Harington, 2011; Schubert & Mead, 2012; Czaplewski et al., 2018, 2022; Moroz et al., 2021; Kottkamp et al., 2022
Eptesicus cf. *fuscus*	PENNSYLVANIA: New Paris No. 4 Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1964
cf. *Eptesicus fuscus*	MISSOURI: Little Beaver Cave	Late Pleistocene, Rancholabrean	Schubert, 2003
Euderma maculatum	ARIZONA: Marble Canyon Cave	Late Pleistocene, Rancholabrean	Mead & Mikesic, 2001
Lasionycteris noctivagans	CANADA: QUEBEC: Mine Cave; ALBERTA: Eagle Cave, Rats Nest Cave; US: OKLAHOMA: Sassafras Cave	Late Pleistocene, Rancholabrean	Czaplewski et al., 2002; Harington, 2011
Lasiurus blossevillii	NEW MEXICO: Carlsbad Cavern	Late Pleistocene, Rancholabrean	Kottkamp et al., 2022; Harris, 2024
Lasiurus borealis	KENTUCKY: Mammoth Cave; WEST VIRGINIA: New Trout Cave, Patton Cave, Hamilton Cave	Late Pleistocene, Rancholabrean	Garton & Grady, 1980, 1988, 1991; Grady et al., 2002; Schubert & Mead, 2012
Lasiurus cf. *borealis*	MISSOURI: Bat Cave; VIRGINIA: Clark's Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1977; Hawksley et al., 1973
Lasiurus borealis or *L. seminolus*	TENNESSEE: Lookout Mountain Cave	Late Pleistocene, Rancholabrean	Gaudin et al., 2011
Aeorestes cinereus	CANADA: ALBERTA: Eagle Cave; US: KENTUCKY: Mammoth Cave; NEW MEXICO: Carlsbad Caverns, Dry Cave[1], Pendejo Cave; TEXAS: Schulze Cave	Late Pleistocene, Rancholabrean	Dalquest et al., 1969; Harris, 2003, 2024; Schubert & Mead, 2012; Kottkamp et al., 2022

Aeorestes cf. *cinereus*	MISSOURI: Bat Cave	Late Pleistocene, Rancholabrean	Hawksley et al., 1973
Lasiurus sp.	NEW MEXICO: Dry Cave[1]	Late Pleistocene, Rancholabrean	Harris, 2024
cf. *Myotis*	ARIZONA: Deadman Cave	Late Pleistocene, Rancholabrean	Mead et al., 2004, 2005
Myotis austroriparius	KENTUCKY: Bat Cave	Late Pleistocene, Rancholabrean	Jansky et al., 2016
Myotis californicus	NEW MEXICO: Dry Cave[1]	Late Pleistocene, Rancholabrean	Harris, 2024
Myotis ciliolabrum	CALIFORNIA: Kokoweef Cave; NEW MEXICO: Carlsbad Cavern; TEXAS: Lower Sloth Cave	Late Pleistocene, Rancholabrean	Reynolds et al., 1991; Kottkamp et al., 2022; Harris, 2024
Myotis californicus or *M. ciliolabrum*	NEW MEXICO: Dry Cave[1]; TEXAS: Dust Cave	Late Pleistocene, Rancholabrean	Harris, 2024
Myotis ciliolabrum or *M. melanorhinus*	IDAHO: Rattlesnake Cave	Late Pleistocene, Rancholabrean	Steadman et al., 1994
Myotis evotis	NEW MEXICO: Dry Cave[1]	Late Pleistocene, Rancholabrean	Harris, 2024
Myotis cf. *evotis*	TEXAS: Schulze Cave	Late Pleistocene, Rancholabrean	Dalquest et al., 1969
Myotis grisescens	KENTUCKY: Bat Cave, Mammoth Cave; MISSOURI: Crankshaft Cave; OKLAHOMA: Three-Forks Cave; TENNESSEE: Lookout Mountain Cave; WEST VIRGINIA: New Trout Cave	Late Pleistocene, Rancholabrean	Parmalee et al., 1969; Garton & Grady, 1980; Grady et al., 2002; Gaudin et al., 2011; Schubert & Mead, 2012; Jansky et al., 2016; Czaplewski et al., 2018
Myotis cf. *grisescens*	MISSOURI: Bat Cave, Brynjulfson Caves 1 & 2; WEST VIRGINIA: Hoffman School Cave	Late Pleistocene, Rancholabrean	Parmalee & Oesch, 1972; Hawksley et al., 1973; Guilday & Hamilton, 1978
Myotis keenii	CANADA: QUEBEC: Trou Otis & Spéos de la Fée Caves; ONTARIO: Elba Cave, Dickson Cave	Late Pleistocene-early Holocene, Rancholabrean-Recent	Harington, 2011
Myotis leibii	KENTUCKY: Bat Cave, Mammoth Cave; TENNESSEE: Cave Without a Name, Lookout Mountain Cave; WEST VIRGINIA: New Trout Cave	Late Pleistocene, Rancholabrean	Garton & Grady, 1980; Grady et al., 2002; Gaudin et al., 2011; Schubert & Mead, 2012; Jansky et al., 2016
Myotis lucifugus	CANADA: QUEBEC: St-Elzéar Cave, Mine Cave, Laflèche Cave; ONTARIO: Elba Cave, Kelso Cave, Mt. Nemo Cave;, ALBERTA: Rats Nest Cave; US: ALABAMA: ACb-2, ACb-3, & ACb-4 Caves, Little Bear Cave; KENTUCKY: Bat Cave, Mammoth Cave	Late Pleistocene, Rancholabrean	Womochel & Barnett, 1980; Ebersole & Ebersole, 2011; Harington, 2011; Schubert & Mead, 2012; Jansky et al., 2016
Myotis cf. *lucifugus*	CANADA, QUEBEC: Saint-Elzéar Cave; MISSOURI: Bat Cave, Crankshaft Cave; PENNSYLVANIA: New Paris no. 4 Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1964; Parmalee et al., 1969; Hawksley et al., 1973; LaSalle, 1984
Myotis †*rectidentis*	TEXAS: *Laubach Cave/Innerspace Cavern	Late Pleistocene, Rancholabrean	Choate & Hall, 1967; Dorsey, 1977; Dalquest & Stangl, 1984
Myotis cf. *rectidentis*	NEW MEXICO: Dry Cave[1]	Late Pleistocene, Rancholabrean	Harris, 2024
Myotis septentrionalis	CANADA: QUEBEC: Mine Cave, Laflèche Cave; ONTARIO: Elba Cave; US: KENTUCKY: Bat Cave, Mammoth Cave; PENNSYLVANIA: New Paris No. 4 Cave; TENNESSEE: Cave Without a Name, Lookout Mountain Cave; WEST VIRGINIA: Patton Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1964; Grady, 1988; Gaudin et al., 2011; Harington, 2011; Schubert & Mead, 2012; Jansky et al., 2016
Myotis sodalis	KENTUCKY: Bat Cave, Mammoth Cave; MISSOURI: Bat Cave	Late Pleistocene, Rancholabrean	Hawksley et al., 1973; Schubert & Mead, 2012; Jansky et al., 2016

Myotis cf. *sodalis*	MISSOURI: Crankshaft Cave	Late Pleistocene, Rancholabrean	Parmalee et al., 1969
	ARIZONA: Arkenstone Cave, Bida Cave, Papago Springs Cave, Pyeatt Cave; CALIFORNIA: Kokoweef Cave; NEW MEXICO: Dry Cave[1], Isleta Cave no. 1, Muskox Cave; TEXAS: Lower Sloth Cave	Late Pleistocene, Rancholabrean	Skinner, 1942; Emslie, 1988; Reynolds et al., 1991; Czaplewski et al., 1999, 2022; Czaplewski & Peachey, 2003; Mead et al., 2005; Harris, 2024
Myotis velifer including *Myotis velifer* †*magnamolaris*	ARIZONA: Kartchner Cavern, Papago Springs Cave; NEW MEXICO: Carlsbad Cavern, Dark Canyon Cave, Dry Cave[1], Muskox Cave, Pendejo Cave, U-Bar Cave; TEXAS: Fowlkes Cave, Hall's Cave, *Laubach Cave/Innerspace Cavern, Lower Sloth Cave, Miller's Cave, Schulze Cave, Upper Sloth Cave, Zesch Cave	Late Pleistocene, Rancholabrean	Skinner, 1942; Patton, 1963; Choate & Hall, 1967; Dalquest et al., 1969; Dorsey, 1977; Dalquest & Stangl, 1984; Harris, 1987, 2003, 2024; Toomey, 1993; Czaplewski et al., 1999; NJC unpublished; Sagebiel, 2010; Moroz et al., 2021; Kottkamp et al., 2022
Myotis cf. *velifer*	ARIZONA: La Tetera Cave	Late Pleistocene, Rancholabrean	Czaplewski et al., this volume
Myotis volans	CANADA: ALBERTA: Eagle Cave; NEW MEXICO: Carlsbad Cavern	Late Pleistocene, Rancholabrean	Harington, 2011; Kottkamp et al., 2022; Harris, 2024
Myotis yumanensis	NEW MEXICO: Carlsbad Cavern	Late Pleistocene, Rancholabrean	Kottkamp et al., 2022; Harris, 2024
Myotis sp.	CANADA: ALBERTA: Eagle Cave; BRITISH COLUMBIA: Charlie Lake Cave, Pellucidar II Cave; US: ALABAMA: ACb-2, ACb-3, & ACb-4 Caves, Little Bear Cave; ALASKA: Multiple caves of Prince of Wales Island; ARIZONA: Arkenstone Cave, Bida Cave, Kartchner Cavern, Papago Springs Cave, Pyeatt Cave, Sandblast Cave and Skull Cave, Stanton's Cave; CALIFORNIA: Antelope Cave; IDAHO: Rattlesnake Cave; ILLINOIS: Meyer Cave; IOWA: Duhme Cave; MISSOURI: Bat Cave, Brynjulfson Caves 1 & 2, Little Beaver Cave; NEVADA: a Mormon Mountain cave; NEW MEXICO: Algerita Blossom Cave, Carlsbad Cavern, Conkling Cavern, Dark Canyon Cave, Dry Cave[1], Pendejo Cave, Sierra Diablo Cave, Slaughter Canyon Cave, U-Bar Cave; OKLAHOMA: Sassafras Cave, Three-Forks Cave; WEST VIRGINA: Hamilton Cave, New Paris No. 4 Cave; TENNESSEE: Baker Bluff Cave, Cave Without a Name, Lookout Mountain Cave; TEXAS: Fowlkes Cave, Lower Sloth Cave, Zesch Cave; UTAH: Crystal Ball Cave; VIRGINIA: Clark's Cave; WEST VIRGINIA: Hoffman School Cave, Mandy Walters Cave, New Trout Cave, Patton Cave	Late Pleistocene, Rancholabrean	Skinner, 1942; Guilday et al., 1964, 1977, 1978; Parmalee, 1967; Parmalee & Oesch, 1972; Hawksley et al., 1973; Guilday & Hamilton, 1978; Garton & Grady, 1980; Womochel & Barnett, 1980; Jefferson, 1982; Heaton, 1985; Harris, 1987, 2003, 2024; Emslie, 1988; Grady, 1988, 1991; Reynolds et al., 1991; Steadman et al., 1994; Czaplewski et al., 1999, 2002, 2018, 2022; Grady et al., 2002; Czaplewski & Peachey, 2003; Heaton & Grady, 2003; Jans-Langel & Semken, 2003; Schubert, 2003; Mead et al., 2005; Sagebiel, 2010; Ebersole & Ebersole, 2011; Gaudin et al., 2011; Harington, 2011; Kottkamp et al., 2022
Nycticeius humeralis	ALABAMA: ACb-2, ACb-3, & ACb-4 Caves, Little Bear Cave; TENNESSEE: Baker Bluff Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1978; Womochel & Barnett, 1980; Ebersole & Ebersole, 2011
Parastrellus hesperus	ARIZONA: Sandblast Cave and Skull Cave	Late Pleistocene, Rancholabrean	Emslie, 1988

Perimyotis subflavus	CANADA: QUEBEC: Laflèche Cave; ONTARIO: Mt. Nemo Cave; US: ILLINOIS: Meyer Cave; IOWA: Duhme Cave; KENTUCKY: Mammoth Cave; MISSOURI: Bat Cave, Brynjulfson Caves 1 & 2; OKLAHOMA: Sassafras Cave, Three-Forks Cave; PENNSYLVANIA: Hamilton Cave; TENNESSEE: Baker Bluff Cave, Cave Without a Name, Lookout Mountain Cave; TEXAS: Schulze Cave; VIRGINIA: Clark's Cave; WEST VIRGINIA: Hoffman School Cave, New Trout Cave, Patton Cave	Late Pleistocene, Rancholabrean	Parmalee, 1967; Dalquest et al., 1969; Parmalee & Oesch, 1972; Hawksley et al., 1973; Guilday & Hamilton, 1978; Guilday et al., 1978; Garton & Grady, 1980; Grady, 1988, 1991; Czaplewski et al., 2002, 2018; Grady et al., 2002; Jans-Langel & Semken, 2003; Gaudin et al., 2011; Harington, 2011; Schubert & Mead, 201
Perimyotis cf. *subflavus*	MISSOURI: Crankshaft Cave; PENNSYLVANIA: New Paris no. 4 Cave	Late Pleistocene, Rancholabrean	Guilday et al., 1964; Parmalee et al., 1969
Perimyotis sp.	ALABAMA: Little Bear Cave; MISSOURI: Little Beaver Cave	Late Pleistocene, Rancholabrean	Womochel & Barnett, 1980; Schubert, 2003
?*Perimyotis* sp.	ALABAMA: ACb-2, ACb-3, & ACb-4 Caves	Late Pleistocene, Rancholabrean	Ebersole & Ebersole, 2011
early/middle PLEISTOCENE[3]			
Canada & US except Florida			
Phyllostomidae			
Desmodus sp.	KENTUCKY: Mammoth Cave	middle Pleistocene, late Irvingtonian	Jegla & Hall, 1962; Santucci et al., 2001; Schubert & Mead, 2012
Molossidae			
Tadarida sp.	KENTUCKY: Mammoth Cave; MARYLAND: Cumberland Cave; WEST VIRGINIA: Hamilton Cave	middle Pleistocene, medial and late Irvingtonian	Jegla & Hall, 1962; Repenning & Grady, 1988; Santucci et al., 2001; Schubert & Mead, 2012; Widga & Colburn, 2015; Eshelman et al., 2025
Tadarida †*constantinei*	NEW MEXICO: *New Cave/Slaughter Canyon Cave	middle Pleistocene, medial Irvingtonian	Lawrence, 1960; Morgan, 2002b; Lundberg & McFarlane, 2006; Kottkamp et al., 2022
Tadarida cf. *brasiliensis*	TEXAS: Fyllan Cave	early Pleistocene, early Irvingtonian	Winkler & Gose, 2003; This paper
Vespertilionidae			
Lasiurus borealis		middle Pleistocene, medial Irvingtonian	Eshelman et al., 2025
?*Myotis* sp.	PENNSYLVANIA: Port Kennedy Cave	Pleistocene, medial Irvingtonian	Cope &Mercer, 1897–1901
Myotis sp.	COLORADO: Porcupine Cave; NEW MEXICO: Slaughter Canyon Cave; TEXAS: Fyllan Cave	early to middle Pleistocene, early to medial Irvingtonian	Winkler & Gose, 2003; This paper
Myotis cf. *grisescens*	MARYLAND: Cumberland Cave	middle Pleistocene, medial Irvingtonian	Gidley & Gazin, 1933, 1938; Eshelman et al., 2025
Myotis leibii	MARYLAND: Cumberland Cave	middle Pleistocene, medial Irvingtonian	Eshelman et al., 2025
Corynorhinus †*alleganiensis*	MARYLAND: *Cumberland Cave	middle Pleistocene, medial Irvingtonian	Gidley & Gazin, 1933, 1938

Eptesicus fuscus †*grandis*	ARKANSAS: Conard Fissure; MARYLAND: *Cumberland Cave	middle to late Pleistocene, Irvingtonian	Brown, 1908; Gidley & Gazin, 1933, 1938
Eptesicus fuscus	NEW MEXICO: Slaughter Canyon Cave	middle Pleistocene, medial Irvingtonian	This paper
Perimyotis subflavus	MARYLAND: Cumberland Cave	middle Pleistocene, medial Irvingtonian	Eshelman et al., 2025
Perimyotis sp.	TEXAS: Fyllan Cave	early Pleistocene, early Irvingtonian	Winkler & Gose, 2003
LATE PLEISTOCENE, Mesoamerica (Mexico & Belize)			
Emballonuridae			
Balantiopteryx io	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Peropteryx macrotis	YUCATÁN: Gruta de Loltún	Late Pleistocene/Holocene	Arroyo-Cabrales & Álvarez, 2003
Mormoopidae			
Mormoops megalophylla	NUEVO LEÓN: Cueva de San Josecito; SAN LUIS POTOSÍ: Cueva de La Presita; YUCATÁN: Gruta de Loltún, Actún Spukil	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003
Pteronotus mexicanus[4]	YUCATÁN: Gruta de Loltún, Actún Spukil	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003
Phyllostomidae[5]			
Macrotinae			
Macrotus californicus	SAN LUIS POTOSÍ: Cueva de La Presita	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Desmodontinae			
Desmodus cf. *draculae*	YUCATÁN: Gruta de Loltún	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Álvarez, 2003
Desmodus †*draculae*	BELIZE: Chiquibul Cave System, Cebada Cave	Late Pleistocene & Holocene	Czaplewski et al., 2003
Desmodus rotundus	YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003
Desmodus †*stocki*	MEXICO: Cerro de Tlapacoya Cave; NUEVO LEÓN: Cueva de La Boca; *Cueva de San Josecito; SAN LUIS POTOSÍ: Cueva de La Presita	Late Pleistocene, Rancholabrean	Ray et al., 1988; Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003
Diphylla ecaudata	YUCATÁN: Gruta de Loltún	Late Pleistocene/Holocene	Arroyo-Cabrales & Álvarez, 2003
Phyllostominae			
Chrotopterus auritus	YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003
Mimon cozumelae	YUCATÁN: Actún Spukil	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Tonatia bakeri	BELIZE: Chiquibul Cave System, Cebada Cave	Holocene?	Czaplewski et al., 2003
Tonatia sp.	QUINTANA ROO: Hoyo Negro cenote	Late Pleistocene, Rancholabrean	Cruz et al., 2024
Glossophaginae			
Choeronycteris mexicana	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Glossophaga soricina	YUCATÁN: Gruta de Loltún	Late Pleistocene/Holocene	Arroyo-Cabrales & Álvarez, 2003

Leptonycteris nivalis	NUEVO LEÓN: Cueva de San Josecito; TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970; Arroyo-Cabrales & Polaco 2003
Leptonycteris yerbabuenae	SAN LUIS POTOSÍ: Cueva de La Presita	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco 2003
Carolliinae			
Carollia subrufa or *C. brevicauda*	BELIZE: Chiquibul Cave System, Cebada Cave	Late Pleistocene/Holocene	Czaplewski et al., 2003
Stenodermatinae			
Artibeus jamaicensis	TAMAULIPAS: Cueva de El Abra; YUCATÁN: Gruta de Loltún, Actún Spukil	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970; Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003;
Artibeus lituratus	BELIZE: Chiquibul Cave System, Cebada Cave	Late Pleistocene/Holocene	Czaplewski et al., 2003
Artibeus sp.	QUINTANA ROO: Hoyo Negro cenote	Late Pleistocene, Rancholabrean	Cruz et al., 2024
Centurio senex	BELIZE: Chiquibul Cave System, Cebada Cave	Holocene?	Czaplewski et al., 2003
Chiroderma villosum	YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003
Dermanura sp.	BELIZE: Chiquibul Cave System, Cebada Cave	Holocene?	Czaplewski et al., 2003
Sturnira lilium	YUCATÁN: Gruta de Loltún; BELIZE: Chiquibul Cave System, Cebada Cave	Late Pleistocene/Holocene	Arroyo-Cabrales & Álvarez, 2003; Czaplewski et al., 2003
Molossidae			
Eumops perotis	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Nyctinomops aurispinosus	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Nyctinomops laticaudatus	TAMAULIPAS: Cueva de El Abra; YUCATÁN: Gruta de Loltún	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970; Arroyo-Cabrales & Álvarez, 2003;
Tadarida brasiliensis	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Tadarida cf. *brasiliensis*			
Tadarida sp.	CHIHUAHUA: Cueva Jiménez	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003; Harris, 2024
Vespertilionidae			
Aeorestes cinereus	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Antrozous pallidus	CHIHUAHUA: Cueva Jiménez	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Polaco, 2003
Corynorhinus townsendii[6]	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Handley, 1955; Jones, 1958; Arroyo-Cabrales & Polaco, 2003;
Dasypterus ega	BELIZE: Cebada Cave, Chiquibul Cave System; YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene, Rancholabrean	Arroyo-Cabrales & Álvarez, 2003; Czaplewski et al., 2003
Dasypterus intermedius	YUCATÁN: Gruta de Loltún	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003; Simmons et al., 2020
Eptesicus furinalis	YUCATÁN: Gruta de Loltún, Actún Spukil	Late Pleistocene & Holocene	Arroyo-Cabrales & Álvarez, 2003; Arroyo-Cabrales & Polaco, 2003
Eptesicus fuscus	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Johnson, 2002
Lasionycteris cf. *noctivagans*	TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970
Lasiurus blossevillii	BELIZE: Chiquibul Cave System, Cebada Cave; NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene & Holocene, Rancholabrean	Arroyo-Cabrales & Johnson, 2002; Czaplewski et al., 2003

Myotis californicus	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Johnson, 2002; Arroyo-Cabrales & Polaco, 2003
Myotis thysanodes	NUEVO LEÓN: Cueva de San Josecito	Late Pleistocene, Rancholabrean	Arroyo-Cabrales & Johnson, 2002; Arroyo-Cabrales & Polaco, 2003
Myotis sp.	CHIHUAHUA: Cueva Jiménez; SAN LUIS POTOSÍ: Cueva de La Presita; TAMAULIPAS: Cueva de El Abra	Late Pleistocene, Rancholabrean	Dalquest & Roth, 1970; Arroyo-Cabrales & Polaco, 2003; Harris, 2024
LATE QUATERNARY[7] West Indies			
Noctilonidae			
Noctilio leporinus	Barbuda; Cuba; Puerto Rico	Late Quaternary[5]	Silva Taboada, 1979; Morgan, 2001
Mormoopdidae			
Mormoops blainvillei	Anguilla#, Antigua#, Bahamas#: Abaco, Exuma, New Providence; Barbuda#; Cuba; Gonâve#; Guadeloupe: Marie-Galante#; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Koopman, 1955; Pregill et al., 1988, 1994; Morgan, 2001; Velazco et al., 2013; Stoetzel et al., 2016
Mormoops †magna	Cuba*; Hispaniola (DR)	Late Quaternary	Silva Taboada, 1974; Velazco et al., 2013
Mormoops megalophylla#	Bahamas: Abaco, Andros; Cuba; Guadeloupe: Marie-Galante#; Hispaniola (DR); Jamaica	Late Quaternary	Morgan, 2001; Silva Taboada, 1974; Stoetzel et al., 2016
Pteronotus macleayi	Bahamas#: New Providence; Cuba; Guadeloupe: Marie-Galante#; Hispaniola (DR)	Late Quaternary	Morgan, 1989, 2001; Silva Taboada, 1974, 1979; Velazco et al., 2013; Stoetzel et al., 2016
Pteronotus parnellii[4]	Antigua#; Bahamas#: Abaco, New Providence: Cayman Islands#: Grand Cayman; Cuba; Guadeloupe: Marie-Galante#; Jamaica	Late Quaternary	Pregill et al., 1988; Morgan, 1994, 2001; Soto-Centeno & Steadman, 2015; Stoetzel et al., 2016
Pteronotus portoricensis	Puerto Rico	Late Quaternary	Morgan, 2001
Pteronotus †pristinus	Cuba*	Late Quaternary	Silva Taboada, 1974
Pteronotus pusillus	GonÂve#, Hispaniola (DR, H)	Late Quaternary	Koopman, 1955; Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Pteronotus quadridens	Bahamas#: Abaco, Andros, New Providence; Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Phyllostomidae[5]			
Macrotinae			
Macrotus waterhousii	Anguilla#, Bahamas: Abaco, Andros, Exuma, New Providence; Barbuda#; CAICOS ISLAMDS: Middle (=Grand) Caicos#; Cayman Islands: Cayman Brac, Grand Cayman; Cuba; Gonâve#; Hispaniola (DR, H); Puerto Rico#, St. Martin#	Late Quaternary[1]	Koopman, 1955; Pregill et al., 1994; Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Desmodontinae			
Desmodus rotundus#	Cuba	Late Quaternary	Koopman, 1958; Orihuela, 2011

Phyllostominae			
Tonatia †saurophila	Jamaica	Late Quaternary	Koopman & Williams, 1951
Glossophaginae			
Brachyphylla cavernarum	Antigua; Guadeloupe: Marie-Galante; Puerto Rico	Late Quaternary	Pregill et al., 1988; Morgan, 2001; Stoetzel et al., 2016
Brachyphylla nana	Bahamas#: Andros; CAICOS ISLANDS: Middle (=Grand) Caicos; Cayman Islands: Cayman Brac#, Grand Cayman; Cuba; Hispaniola (DR, H); Jamaica#	Late Quaternary	Koopman & Williams, 1951; Silva Taboada, 1979; Morgan, 1989, 1994, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Erophylla bombifrons	Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Erophylla sezekorni	Bahamas: Abaco, Andros, Exuma, New Providence; Cayman Islands: Cayman Brac, Grand Cayman; Cuba; Jamaica	Late Quaternary	Silva Taboada, 1979; Morgan, 1989, 1994, 2001
Glossophaga soricina	Jamaica	Late Quaternary	Koopman & Williams, 1951
Monophyllus plethodon	Antigua; Guadeloupe: Marie-Galante; Puerto Rico#	Late Quaternary	Choate and Birney 1968; Morgan, 2001; Stoetzel et al., 2016
Monophyllus redmani	Bahamas#: Abaco, Andros, New Providence; CAICOS ISLANDS: Middle (=Grand) Caicos; Cayman Islands#: Grand Cayman; Cuba; Gonâve#; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Phyllonycteris aphylla	Jamaica	Late Quaternary	Koopman & Williams, 1951
Phyllonycteris †major	Antigua; Guadeloupe: Marie-Galante; Puerto Rico	Late Quaternary	Pregill et al., 1984; Morgan, 2001; Simmons et al., 2020; Stoetzel et al., 2016
Phyllonycteris poeyi	Bahamas#: Abaco, New Providence; Cayman Islands#: Cayman Brac; Cuba; Hispaniola (DR, H)	Late Quaternary	Silva, 1979; Morgan, 1989, 1994, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Stenodermatinae			
Ardops nichollsi	Guadeloupe: Marie-Galante	Late Quaternary	Stoetzel et al., 2016
Ariteus flavescens	Jamaica	Late Quaternary	Koopman & Williams, 1951
Artibeus †anthonyi	Cuba	Late Quaternary	Silva Taboada, 1979; Morgan, 2001
Artibeus jamaicensis	Cuba; Gonâve; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Koopman, 1955; Silva Taboada, 1979; Morgan, 2001
†Cubanycteris silvai	Cuba	Late Quaternary	Mancina & García-Rivera, 2005
Phyllops falcatus	Cuba, Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Phyllops †silvai	Cuba	Late Quaternary	Suárez & Díaz-Franco, 2003
Phyllops †vetus	Cuba	Late Quaternary	Morgan, 2001
Stenoderma rufum	Puerto Rico	Late Quaternary	Choate & Birney, 1968
Natalidae			Tejedor, 2011
Chilonatalus macer	Cayman Islands#: Grand Cayman; Cuba	Late Quaternary	Morgan, 2001; Tejedor, 2011

Chilonatalus micropus	Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Tejedor, 2011; Velazco et al., 2013; Soto-Centeno et al., 2017
Chilonatalus tumidifrons	Bahamas: Andros, Cat#, Exuma#, New Providence#	Late Quaternary	Morgan, 1989, 2001
Natalus jamaicensis	Jamaica	Late Quaternary	Koopman & Williams, 1951; Tejedor, 2011;
Natalus major[8]	Guadeloupe: Marie-Galante#; Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Tejedor, 2011; Stoetzel et al., 2016; Soto-Centeno et al., 2017
Natalus primus	Bahamas#: Abaco, Andros, Eleuthera, New Providence: Caicos Islands: Middle (=Grand) Caicos#; Cayman Islands#: Grand Cayman; Cuba	Late Quaternary	Morgan, 2001; Tejedor, 2011
Natalus stramineus[8]	Guadeloupe: Marie-Galante	Late Quaternary	Stoetzel et al., 2016
Nyctiellus lepidus	Bahamas: Andros#, Exuma; Cuba	Late Quaternary	Silva Taboada, 1979; Morgan, 2001
Molossidae			
Molossus molossus	Antigua; Guadeloupe: Marie-Galante; Jamaica;	Late Quaternary	Koopman & Williams, 1951; Pregill et al., 1988; Stoetzel et al., 2016
Nyctinomops macrotis	Cuba; Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Soto-Centeno et al., 2017
Tadarida brasiliensis	Antigua; Bahamas: Abaco, New Providence#; Cayman Islands: Grand Cayman; Cuba; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Morgan, 2001; Soto-Centeno et al., 2017
Vespertilionidae			
Aeorestes cinereus	Hispaniola (H)	Late Quaternary	Soto-Centeno et al., 2017
Antrozous koopmani[9]	Cuba	Late Quaternary	Silva Taboada, 1979; Morgan, 2001; Orihuela et al., 2020
Dasypterus insularis	Cuba; Hispaniola (DR#)	Late Quaternary	Silva Taboada, 1979; Morgan, 2001
Eptesicus fuscus	Bahamas: Abaco, Andros, Exuma New Providence; Cayman Islands: Grand Cayman, Cayman Brac; Cuba; Hispaniola (DR, H); Jamaica; Puerto Rico	Late Quaternary	Morgan, 2001; Velazco et al., 2013; Soto-Centeno et al., 2017
Lasiurus minor	Hispaniola (DR, H)	Late Quaternary	Morgan, 2001; Soto-Centeno et al., 2017
Lasiurus pfeifferi	Cuba	Late Quaternary	Silva Taboada, 1979; Morgan, 2001
Myotis cf. *austroriparius*#	Bahamas: Abaco	Late Pleistocene	Morgan, 2001; Soto-Ceteno & Steadman, 2015
Florida Karst Deposits[10] **Late Pleistocene**			
Phyllostomidae			
Desmodus †*stocki*	Arredondo 2A, Haile 1A, Haile 11B, Reddick 1A, 1B, 1C	Late Pleistocene, Rancholabrean	Morgan, 1991

Mormoopidae			
Mormoops megalophylla#	Cutler Hammock, Monkey Jungle Hammock, Rock Springs	Late Pleistocene, Rancholabrean	Ray et al., 1963; Wilkins, 1983; Morgan, 1991, 2002
Pteronotus †*pristinus*	Monkey Jungle Hammock	Late Pleistocene, Rancholabrean	Morgan, 1991, 2002
Molossidae			
Eumops floridanus	Monkey Jungle Hammock	Late Pleistocene, Rancholabrean	Martin, 1977; Morgan, 1991, 2002
Eumops underwoodi#	Lecanto 2A	Late Pleistocene, Rancholabrean	Morgan, 1991
Tadarida brasiliensis	Monkey Jungle Hammock, Reddick 1A	Late Pleistocene, Rancholabrean	Morgan, 1991
Vespertilionidae			
Eptesicus fuscus	Arredondo 2A, Cutler Hammock, Monkey Jungle Hammock, Reddick 1	Late Pleistocene, Rancholabrean	Morgan, 1991
Lasiurus borealis/*L. seminolus*	Monkey Jungle Hammock, Reddick 1	Late Pleistocene, Rancholabrean	Morgan, 1991
Dasypterus intermedius	Arredondo 2A, Devil's Den, Haile 11B, Reddick 1	Late Pleistocene, Rancholabrean	Martin & Webb, 1974; Morgan, 1991
Myotis austroriparius	Arredondo 2A, Cutler Hammock, Devil's Den, Reddick 1, Rock Springs	Late Pleistocene, Rancholabrean	Martin & Webb, 1974; Morgan, 1991
Myotis grisescens	Devil's Den, Surprise Cave	Late Pleistocene, Rancholabrean	Martin & Webb, 1974; This paper
Nycticeius humeralis	Cutler Hammock, Monkey Jungle Hammock	Late Pleistocene, Rancholabrean	Morgan, 1991
Perimyotis subflavus	Devil's Den, Haile 11B, Lecanto 2A, Reddick 1	Late Pleistocene, Rancholabrean	Martin & Webb, 1974; Morgan, 1991
Florida Karst Deposits Early and Middle Pleistocene			
Phyllostomidae			
Desmodus †*archaeodaptes*	Inglis 1A Haile 16A, Haile 21A*	early Pleistocene, late Blancan early Pleistocene, early Irvingtonian	Morgan et al., 1988
Vespertilionidae			
Antrozous sp.#	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Corynorhinus rafinesquii	Coleman 2A	middle Pleistocene, late Irvingtonian	Martin, 1974
Corynorhinus sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Eptesicus sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Lasiurus sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Myotis cf. *austroriparius*	Haile 16A, Haile 21A Coleman 2A	early Pleistocene, early Irvingtonian middle Pleistocene, late Irvingtonian	Morgan, 1991 Martin, 1974
Myotis sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Perimyotis subflavus	Coleman 2A	middle Pleistocene, late Irvingtonian	Martin, 1974

Perimyotis sp.	Inglis 1A	early Pleistocene, late Blancan	Morgan, 1991
Florida Karst Deposits Oligocene and Miocene			
Emballonuridae			
†*Floridopteryx poyer*i	Thomas Farm*	early Miocene, early Hemingfordian	Morgan & Czaplewski, 2023
†*Oligopteryx floridanus*	I-75 Brooksville 2*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Morgan & Czaplewski, 2023
†*Oligopteryx hamaxitos*	I-75 Brooksville 2*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Morgan & Czaplewski, 2023
†*Karstopteryx gunnelli*	Buda*	latest Oligocene, late Arikareean	Morgan & Czaplewski, 2023
†Speonycteridae[11]			
†*Speonycteris aurantiadens*	I-75 Brooksville 2*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Czaplewski & Morgan, 2012
†*Speonycteris naturalis*	I-75*	early Oligocene, Whitneyan	Czaplewski & Morgan, 2012
Mormoopidae[5]			
†*Koopmanycteris palaeomormoops*	I-75 Brooksville 2*	early Oligocene, Whitneyan late Oligocene, early Arikareean	Morgan et al., 2019
Natalidae			
†*Primonatalus prattae*	Thomas Farm*	early Miocene, early Hemingfordian	Morgan & Czaplewski, 2003
genus and species indet.	I-75	early Oligocene, Whitneyan	Morgan & Czaplewski, 2003
Molossidae			
Tadarida/*Mormopterus* sp. indet. 1	Thomas Farm	early Miocene, early Hemingfordian	Czaplewski et al., 2000b
Tadarida/*Mormopterus* sp. indet. 2	Thomas Farm	early Miocene, early Hemingfordian	Czaplewski et al., 2000b
genus & species indet.	Brooksville 2	late Oligocene, early Arikareean	Czaplewski et al., 2000b
Vespertilionidae			
†*Karsta silva*	Thomas Farm*	early Miocene, early Hemingfordian	Czaplewski & Morgan, 2000
†*Miomyotis floridanus*	Thomas Farm*	early Miocene, early Hemingfordian	Lawrence, 1943
†*Suaptenos whitei*	Thomas Farm*	early Miocene, early Hemingfordian	Lawrence, 1943
lasiurine, undesc. genus & species	Thomas Farm	early Miocene, early Hemingfordian	Morgan & Czaplewski, 2023
plecotine, undesc. genus & species	Thomas Farm	early Miocene, early Hemingfordian	Morgan & Czaplewski, 2023
genus & species indet.	I-75	early Oligocene, Whitneyan	Morgan & Czaplewski, 2023

[1] States of the US and Mexico are in upper case letters, as are Belize in Central America. Because our paper focuses primarily on continental North America and there are several hundred cave sites in the West Indies that have produced fossil bats, we do not list individual cave sites in the West Indies, only the islands on which the bat species have been reported. See Morgan (2001) for references to most of the individual cave sites from which these species are known, with more recent updates in Dávalos and Turvey (2012), Velazco et al. (2013), Soto-Centeno and Steadman (2015), Stoetzel et al (2016), and Soto-Centeno et al. (2017).

[2] Dry Cave, New Mexico, US, includes sublocalities published as Animal Fair, Balcony Room, Bison Chamber, Harris' Pocket, Lost Valley, Room of the Vanishing Floor, and Sabertooth Camel Maze (Harris, 1985; 2024).

[3] We recognize the subdivisions of the Irvingtonian NALMA of Bell et al. (2004) as follows: Irvingtonian I (=early Irvingtonian), 0.85-1.72 Ma; Irvingtonian II (=medial Irvingtonian), 0.4-0.85 Ma; Irvingtonian III (=late Irvingtonian). 0.4-0.15 Ma.

[4] Pavan and Marroig (2016) recognized eight species formerly included within the species *Pteronotus parnellii*, two of which occur in Mesoamerica, *P. mexicanus* and *P. mesoamericanus*, and three of which occur the West Indies, *P. parnelii* s.s., *P. portoricensis,* and *P. pusillus*. *P. parnellii*, as recognized by Pavan and Marroig (2016), occurs only in Cuba and Jamaica, with fossil records from both islands noted here. No member of the *P. parnellii* species group occurs at present in the Bahamas, Cayman Islands, or Lesser Antilles, so we have left the fossil records from these islands under *P. parnellii*, until they can be studied further to determine their correct species allocation.

[5] We subdivide the Phyllostomidae into subfamilies following Baker et al. (2016). The order of subfamilies follows the phylogeny in Baker et al. (2016); genera and species within each subfamily are in alphabetical order.

[6] Originally described as an extinct species, *Corynorhinus tetralophodon* (Handley, 1955), but synonymized with *C. townsendii* by Arroyo-Cabrales and Johnson (2002).

[7] For the West Indies only, both late Pleistocene and Holocene fossil bats are combined under the broader time category of Late Quaternary, with most fossil bats from this region probably Holocene in age. The few bat bones from the West Indies that have been directly radiocarbon dated are Holocene (e.g., seven species of bats from Ralph's Cave, Abaco, Bahamas with ^{14}C AMS dates ranging from 1,810–3,740-yr BP; Soto-Centeno and Steadman, 2015). Late Pleistocene dates ranging from 11,348–34,600 yr BP were associated with fossil bats from Blanchard Cave, Marie-Galante, but the dates were analyzed using guano not bat bones (Stoetzel et al., 2016).

[8] Varona (1974) and Koopman (1989) recognized a single species of large *Natalus*, *N. stramineus*, from the West Indies. Morgan (2001) limited *N. stramineus* to the Lesser Antilles and recognized a larger species, *N. major*, from the Greater Antilles. Tejedor (2011) split the large species of *Natalus* from the West Indies into four species, *N. jamaicensis* from Jamaica, *N. major* from Hispaniola, *N. primus* from Cuba, and *N. stramineus* from the Lesser Antilles. Tejedor (2011) referred extirpated populations of a large *Natalus* from the Bahamas, Middle (=Grand) Caicos, and Grand Cayman to *N. primus*.

[9] We recognize *Antrozous koopmani* as a valid species following Orihuela et al. (2020). Other publications consider *A. koopmani* to be a subspecies of the mainland *A. pallidus* (Simmons, 2005).

[10] Late Pleistocene deposits from Florida include bats from one underwater cave (Devil's Den), one underwater spring (Rock Springs), and one dry cave (Surprise Cave). All other Florida fossil sites listed here are karst deposits.

[11] The extinct family Speonycteridae and the extant family Mormoopidae, together with the extant families Phyllostomidae, Noctilionidae, and Thyropteridae are placed in the superfamily Noctilionoidea.