

LATE PLEISTOCENE VERTEBRATES FROM THREE-FORKS CAVE, ADAIR COUNTY, OKLAHOMA OZARK HIGHLAND

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Abstract

We report on an assemblage of vertebrate fossils from a limestone cave in the southwestern portion of the Ozark Highlands. The fauna includes several extinct, large-bodied mammalian taxa including *Megalonyx jeffersonii* (Jefferson's ground sloth), *Canis dirus* (dire wolf), *Arctodus simus* (short-faced bear; two individuals), and Equidae (extinct horses), which indicate a late Pleistocene age. In addition, there is a variety of extant vertebrates including a fish, *Aplodinotus* cf. *grunniens* (freshwater drum), unidentified Anura (frogs and toads) and Caudata (salamanders), *Terrapene* sp. (box turtles), cf. *Ophisaurus* (legless lizards), Colubroidea and Crotalidae (non-venomous snakes and pit vipers), *Bubo virginianus* (great horned owl), and at least 12 other mammals: *Sorex* sp. (long-tailed shrews), *Perimyotis subflavus* (tricolored bat), *Eptesicus fuscus* (big brown bat), *Myotis grisescens* (gray myotis), possibly other species of *Myotis*, Vulpini (foxes), several rodents, *Geomys* sp. (pocket gophers), *Chaetodipus* or *Perognathus* (pocket mice), Peromyscini (native mice), *Neotoma* cf. *floridana* (eastern wood rat), *Microtus* cf. *ochrogaster* (prairie vole), and, *Sylvilagus* sp. (cottontail rabbits). An earlier report provided a tentative age of one of the *Arctodus simus* of about 34,000 years ago (late Pleistocene, Rancholabrean). Among the 23 taxa in the Three-Forks Cave assemblage, two species are added to the Oklahoma Ozark Highland paleofauna: freshwater drum and great horned owl. One extralimital taxon, the pocket mouse *Chaetodipus* or *Perognathus*, is present in the assemblage. Numerous remains of juvenile bats of *Myotis grisescens* and *Eptesicus fuscus* provide evidence that these species used Three-Forks Cave as a maternity site. Large crater-like pits in the floor of Three-Forks Cave and other caves in the vicinity may represent ancient and modern beds of the short-faced bear and black bear, respectively.

Introduction

Late Pleistocene faunas are relatively well known from localities in the Ozark Highlands of central North America, especially those recovered from caves. In the online database for North American late Quaternary mammal localities, FAUNMAP II-NEOTOMA (FAUNMAP Working Group, 1994; <http://www.ucmp.berkeley.edu/faunmap/about/index.html>), 36 such vertebrate faunal assemblages are known in the Missouri Ozarks and four in the Arkansas Ozarks. No localities from the Oklahoma portion of the Ozark Highland are listed in FAUNMAP II-NEOTOMA, but three cave sites were overlooked. These are Gittin' Down Mountain Cave (an alternative name for Three-Forks Cave) with one species (Puckette, 1976; Smith and Cifelli, 2000), Sassafra Cave with nine taxa (Czaplewski et al., 2002); and CZ-9 Cave (aka Dressler Cave) with three taxa (Czaplewski and Puckette, 2015). Three-Forks Cave, with 23 taxa described herein, substantially adds to the Pleistocene fauna of the Ozark Highland in Oklahoma and bolsters knowledge of the Quaternary history of this physiographic region.

A single tooth of the short-faced bear, *Arctodus simus*, was reported from Gittin' Down Mountain Cave, Okla. by Puckette (1976). The specimen, a worn right m2, was deposited in the University of Arkansas Museum as UAM 75-839-1. We report additional remains of this same individual bear, as well as a second individual and an associated late Quaternary vertebrate assemblage from the same cave, aka Three-Forks Cave. The *Arctodus* molar from Three-Forks Cave was used by Schubert (2010) in his study of the chronology of late Quaternary *Arctodus* finds in North America. He provided a date of $34,063 \pm 460$ rcybp (NZA-27,734; 14C range at 2 sigma: 33,143 to 34,983 ybp) on the *Arctodus* m2 dentine, but noted that "The C:N ratio of 2.4 falls outside the range of well-preserved collagen.... Further, the percent C is particularly low, and these factors imply that the collagen from the sampled dentine is degraded. While this does not indicate a 'bad' date, it does mean that some degree of caution should be associated with it" (Schubert, 2010: p. 191). If the Three-Forks Cave *Arctodus* date is taken at face value, it is approximately equivalent to the oldest directly-dated *Arctodus simus* in North America from Island Ford Cave, Virginia (in which the collagen was well preserved; Schubert 2010). We, tentatively, use Schubert's (2010) 34 ka date as the approximate age for the Three-Forks Cave assemblage, while pointing out that fossils were collected from several different parts of the cave, and they are likely to be diachronous (Semken et al., 2010).

Three-Forks Cave is on private property adjacent to the Donald R. Russell Cave Preserve, in Adair County, Okla. (Fig. 1), and it is recorded as Oklahoma Museum of Natural History (OMNH) locality V1474. It developed within limestone

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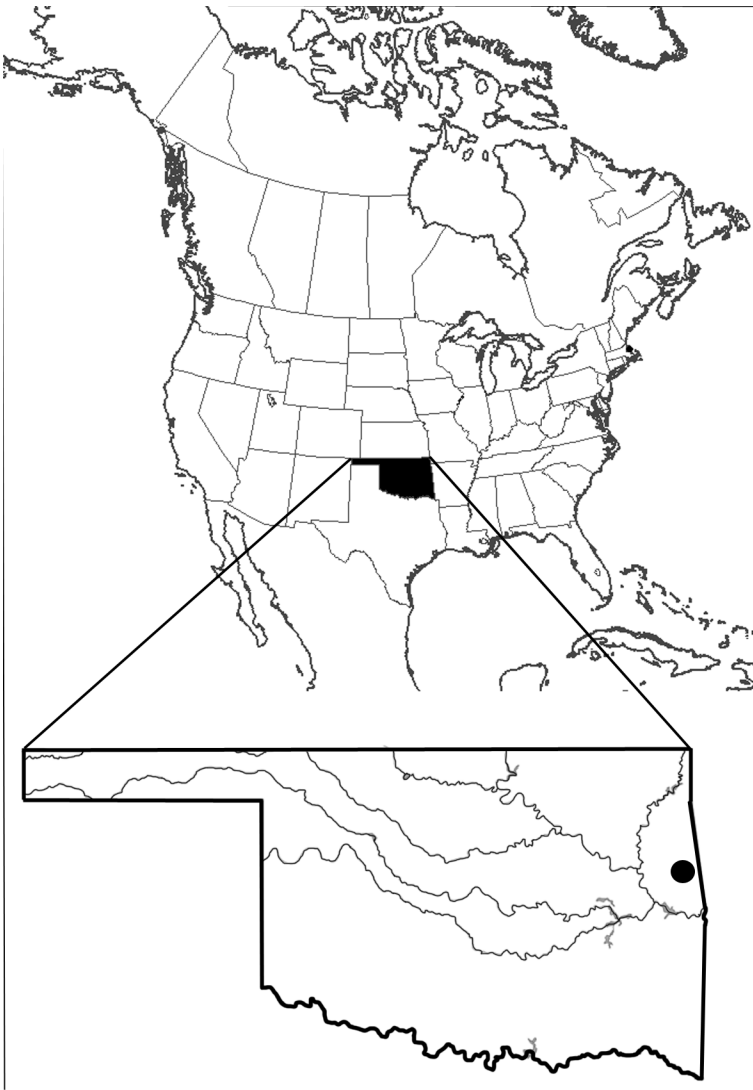


Figure 1. Locator map of central North America with state of Oklahoma in black, enlarged below, showing location of Three-Forks Cave (dot).

many are encrusted in yellowish-buff to brown carbonate with included pebbles and cobbles. In contrast, bones from the Second Parachute Room are mostly light in color with dark-tinted edges, where they had been partly exposed by foot traffic in a walking passage. These bones are more fragmentary and were found in mud on the cave floor. The isolated bones from other areas of the cave vary in color. The dissimilar preservation probably reflects varying conditions in different areas of the cave.

Methods

Specimens were collected on three trips during 2003, 2004, and 2006, using rock hammer, awls, trowels, and chisels. Fossils were selectively removed from carbonate and gravelly mud deposits in the wet crawlways and stream beneath the floor and a natural bridge at the Drain, and in the floor of the Second Parachute Room. They were also removed from rock and mud in the floor at a few other passages. Fossils were wrapped, bagged, and labeled for transport to the OMNH, where they underwent preparation and cleaning. Bulk samples of sedimentary deposits amounting to perhaps 100 kg from the Drain and Second Parachute Room were bagged for transport and processed to recover microvertebrate fossils by standard screenwashing methods using tandem screen boxes of 1.5 mm (coarse) and 0.6 mm (fine) mesh (Cifelli, 1996).

Measurements of larger specimens were made with dial calipers; smaller specimens were measured with an eyepiece reticle in an Olympus SZX9 stereomicroscope. All measurements are in millimeters. Standard measurements of teeth are abbreviated APL for greatest anteroposterior length of crown, and TW for greatest transverse width of crown. Other measurements are described in the text and tables. Of the total of 988 vertebrate specimens recovered from

of the Pitkin Formation, late Mississippian age; the formation is about 18 m thick in this area. Within the cave there are two main bone accumulation areas, the Drain (Fig. 2A) and the Second Parachute Room (Fig. 2B), as well as a few additional isolated occurrences of fossils elsewhere (Fig. 2C, 2D). The Drain is an area in which the small stream running through this part of the cave drops through the floor downstream of several rimstone dams. Numerous small bones that had been cemented into the floor are exposed. From the dams, the stream drops into lower level passages too small to be entered. Many of the larger vertebrates, each of which was represented by an isolated bone, and most of the microvertebrate fossils came from the Drain area (Fig. 2A). The Second Parachute Room is named for a fringed canopy speleothem in the passage. The more complete fossils of two short-faced bears came from the Second Parachute Room (Fig. 2B), while the other bear bones came from a passage not far from the Drain (Fig. 2D). The provenience data for all cave fossils were recorded with individual, cataloged specimens and are also recorded below in the systematic accounts (under Materials). The preservation and condition of fossils in these distinctive areas of the cave differs somewhat, and even varies within one area (microvertebrates in the Drain). Although the temporal span during which fossils accumulated in these cave areas probably also differ, the assemblage is considered a single local fauna.

Some Three-Forks Cave fossils were collected by Clayton and Donald Russell in the mid-late 20th century. We did further collecting in April, 2003, May, 2004, and May, 2006, resulting in a total of 988 cataloged specimens. Most of the bones from the Drain are dark brown to reddish brown, and

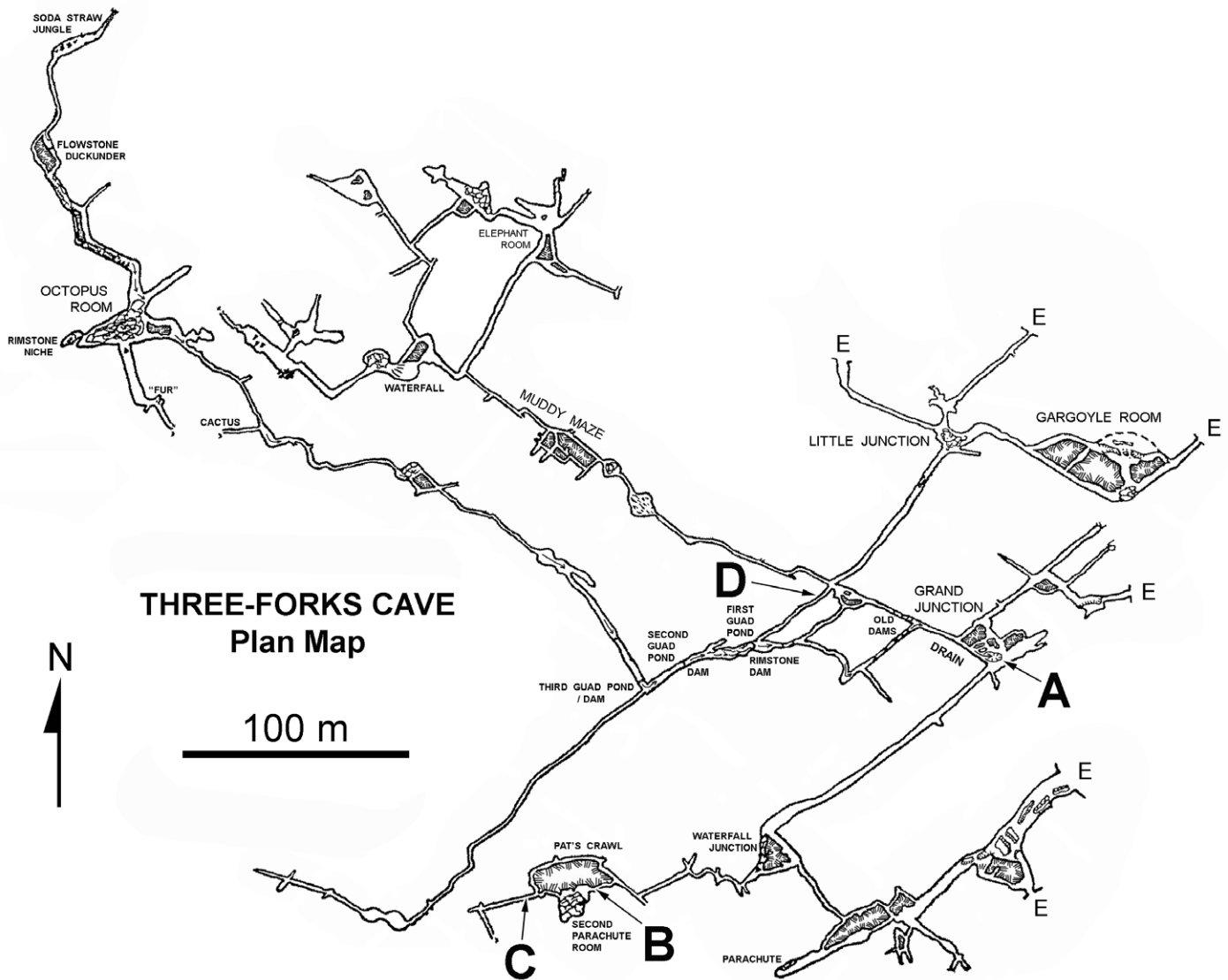


Figure 2. Plan map of Three-Forks Cave, Adair County, Oklahoma, by Donald Russell, 1976, indicating areas in which fossils in this report were recovered. Abbreviations: A, main concentration of fossils, including most microvertebrates, within the Drain; B, concentration of *Arctodus simus* bones and a few microvertebrates near Second Parachute Room; C, isolated horse bone; D, isolated *Arctodus* bones; E, entrances; Small Arrows within cave passages indicate present stream flow to the Drain.

Three-Forks Cave, about 840 are bats (85% of cataloged specimens) of which 700 were identified only to the family level. Herein we list the taxa recovered, with discussion of only those identifiable to lower-level categories (family, genus, or species) or with implications of paleontological significance. A complete inventory of cataloged and identified vertebrate skeletal elements recovered from Three-Forks Cave, Adair County, Okla., is available from the Department of Vertebrate Paleontology at the OMNH.

Systematic Paleontology

Osteichthyes

Sciaenidae

Aplodinotus cf. *grunniens* (freshwater drum)

Material: OMNH 78544, partial premaxilla (Fig. 3A) from the Drain.

The lateral branch of the bone and crowns of the teeth are broken away, but the remainder of the premaxilla, with cuplike tooth bases, is nicely preserved. A few other fish bones, all from the Drain, were recovered but were not identifiable to family. We did not have access to comparative osteological fish specimens. Morphology of the premaxilla resembles that of other sciaenids: having the ascending process rising at a right angle to the alveolar process, ascending process slender and straight and closely appressed to, but separated from, the articular process by a distinct notch, and

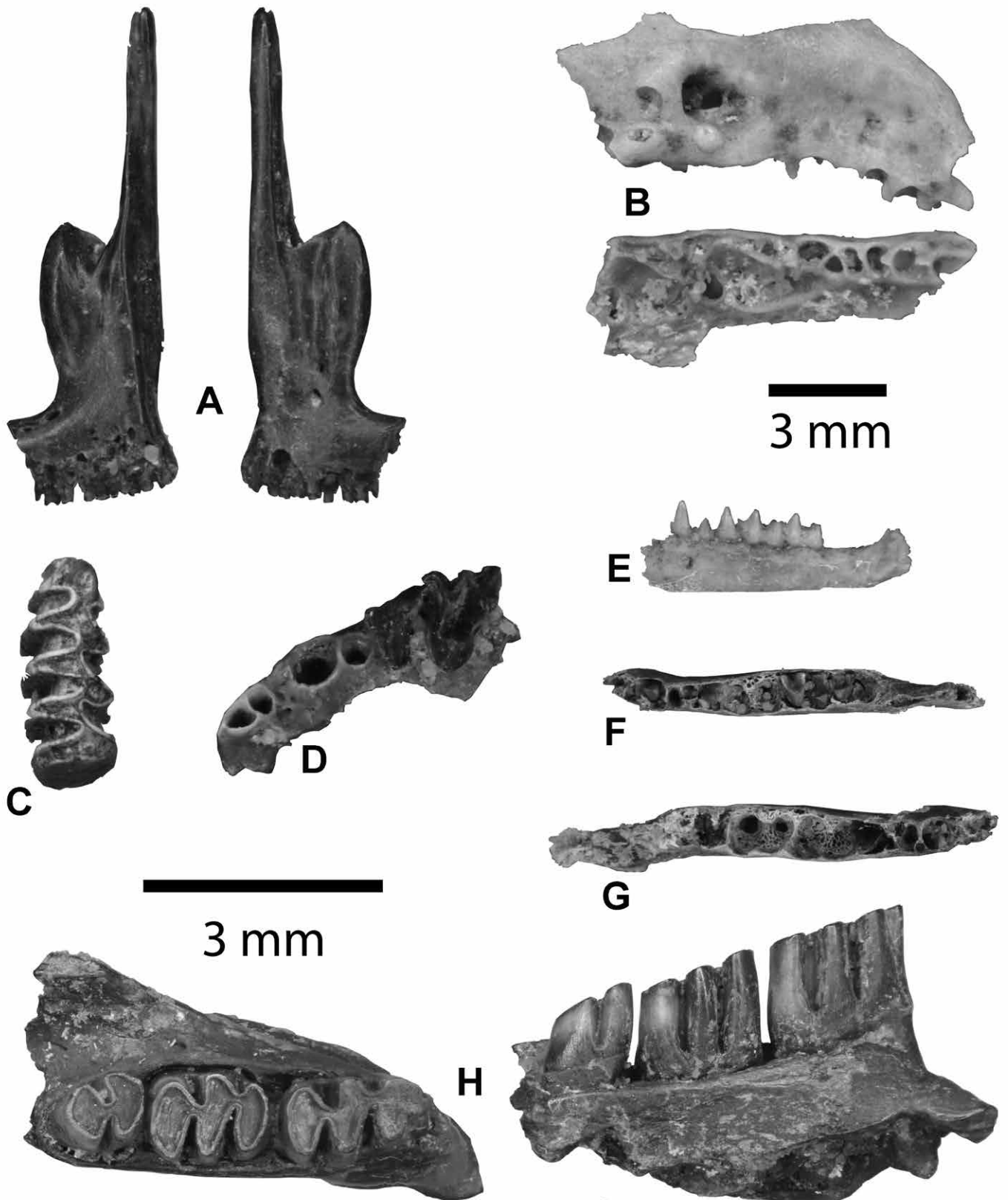


Figure 3. Selected microvertebrate fossils from Three-Forks Cave, Oklahoma. A, *Aplodinotus* cf. *grunniens* right premaxilla (OMNH 78544) in medial and lateral views. B, *Sorex* sp. rostrum fragment (OMNH 78524) in labial and occlusal views. C, *Microtus* cf. *ochrogaster* m1 from dentary fragment (OMNH 78353) in occlusal view. D, *Perimyotis subflavus* rostrum fragment with empty alveoli and P4-M1 (OMNH 77789) in occlusal view; E, *P. subflavus* dentary with c1-m2 (OMNH 77695) in labial view. F, *Myotis grisescens* juvenile dentary with deciduous and permanent tooth alveoli and developing teeth (OMNH 77728) in occlusal view. G, *Eptesicus fuscus* juvenile dentary showing deciduous tooth alveoli and developing permanent teeth (OMNH 77729) in occlusal view. H, *Neotoma* cf. *floridana* dentary fragment with m1-m3 (OMNH 77700) in occlusal and labial views. Scale bar at left pertains to A, C, D, and H; scale bar at right pertains to B, E, F, and G.

articular process about half the height of the ascending process. However, no autapomorphies of the premaxilla are recorded in *Aplodinotus* (Sasaki, 1989). The specimen from Three-Forks Cave matches the premaxilla of the freshwater drum illustrated by Green (1941: plate I fig. 10), Sasaki (1989: fig. 34A), and Qadri and McAllister (1967: plate II fig. 11c). The freshwater drum is distinct among the Sciaenidae as the only member of this large family to inhabit freshwater (Sasaki, 1989); all other Sciaenidae are marine. The recent native distribution of *A. grunniens* includes relatively large bodies of water in the Mississippi River drainage and Great Lakes regions over much of the eastern United States, including the entire Ozark Highlands and surrounding regions (Page and Burr, 1991). If the fossil actually represents the living species and not an unrecognized, extinct one, this is the first fossil record of *A. grunniens* from the Ozark Highlands. The species is relatively common as a Pleistocene fossil in the United States (Jacquemin et al., 2016) and is known as a fossil elsewhere in Oklahoma in the early Pleistocene (Irvingtonian land mammal age) Berends local fauna (Smith, 1954). However, because of our inability to find autapomorphic characters in the fossil, its paleogeographic significance is dubious.

Amphibia

Anura

Sixteen skeletal elements, including several ilia, from an undetermined number of individual frogs or toads were recovered from the Drain but lacked morphological characters by which they could be further identified.

Caudata

A total of 45 salamander skeletal elements including several vertebrae were recovered from the Drain. The vertebrae of salamanders are considered taxonomically useful (Holman, 1995). They are identifiable as salamanders, based on the hourglass-shaped centrum and two elongated rib-bearing processes on either side, and on being amphicoelous or with ossified caps on some cotyles as in Plethodontidae. The specimens from Three-Forks Cave could not be identified to family level, but both simple and complex forms noted by Holman (1995) are represented. They are important in providing a basis for inclusion of Caudata in the faunal list.

Reptilia

Chelonia

Emydidae

Terrapene sp. indet. (box turtle)

Material: OMNH 77923, costal bone from the Drain.

The costal is long and narrow, parallel-sided along the sutures with adjacent costals, and curved to indicate a high-domed carapace. It shows grooves proximally for parts of two overlying neural scutes, but no groove for the pleural scutes. Probably, it represents a left fifth costal. These characteristics agree with those of box turtles and differ from costals of other Quaternary genera of North American turtles (Sobolik and Steele, 1996).

Squamata

Anguidae

cf. *Ophisaurus* sp. (glass lizards)

Material: OMNH 78540, osteoderm from the Drain.

The osteoderm is quadrate in outline, unkeeled, thin, with a rugose surface and fairly matches the mid-trunk, dorsal osteoderms of various anguids (Mead et al., 1999). Given the intra- and interindividual morphological variation in osteoderms of these lizards, we can only tentatively refer the isolated specimen to cf. *Ophisaurus*.

Serpentes

Colubroidea indet. (non-venomous snakes)

Material: OMNH 73029-73030, two partial trunk vertebrae from the Drain.

These vertebrae are diagnostic of snakes in possessing zygosphenes and zygantra. They resemble certain North American colubroids in lacking a long, stout hypapophysis; instead they bear low, flattened, spatulate to gladiate, hemal keels (Holman, 2000).

Crotalidae (pit vipers)

Genus indet.

Material: OMNH 78545, trunk vertebra from the Drain.

This vertebra is identifiable as that of a crotalid based on the stout, long hypapophysis (Holman, 2000). The morphological variability of crotalid vertebrae is such that individual vertebrae are not reliably identifiable beyond the family level (Bell et al., 2004). The element could feasibly represent a member of either *Agkistrodon* or *Crotalus*, but is too large (neural arch width, 7.8 mm; width across post-zygapophyses, 11.5 mm) to represent a member of *Sistrurus*.

Aves

Strigiformes

Strigidae

Bubo virginianus (great horned owl)

Material: OMNH 77903, complete right humerus from the Drain.

Measurements (mm) of the specimen are: length, 132.1; width of shaft, 9.3; width of proximal end, 22.6; width of distal end, 10.9. These measurements are well within the ranges of the same measurements for the species provided in Avian Osteology — Bird Bone Identification Guide (https://royalbcmuseum.bc.ca/Natural_History/Bones/Species-Pages/GHOW.htm).

There is some damage proximally to the medial crest and internal tuberosity (tuberculum ventrale). OMNH 77903 is smaller than the humerus of the snowy owl, *Bubo scandiaca*, and great gray owl, *Strix nebulosa*, and larger than that of the barred owl, *Strix varia* and other small North American owls. Morphologically, the humerus differs from that of *Strix* owls in that the ectepicondylar prominence is papilla-shaped and is distinct from the shaft and ectepicondyle (epicondylus dorsalis) (Howard, 1929). It differs from the humerus of the related *B. scandiaca* in having the ectepicondylar prominence shorter relative to its length (Howard, 1929).

This is the first fossil record of the great horned owl in the Ozark Highlands and in Oklahoma. As a late Pleistocene fossil in North America, the species *B. virginianus* is widespread and recorded from sites in the Mexican states of Chihuahua and Nuevo León, and in Arizona, California, Florida, Nevada, New Mexico, Texas, Utah, and Wyoming in the United States (Miller and DeMay, 1942; Miller, 1943; Howard, 1952; Emslie, 1985; Emslie and Heaton, 1987; Hulbert, 2001; Brasso and Emslie, 2006; Harris, 2014).

Mammalia

Xenarthra

Megalonychidae

Megalonyx jeffersonii (Jefferson's ground sloth)

Material: OMNH 77904, either manual digit IV phalanx 2 or manual digit III phalanx 2, lacking the proximal epiphysis, indicating a subadult individual (Fig. 4D–H). From the Drain. Measurements (mm) are greatest depth of distal condyles, 28.7; distal width, 19.4

Because the specimen lacks the proximal epiphysis, the proximal articular surface is absent and cannot be characterized. Adjacent to the growth plate, the dorsoventral height of the bone shaft is less deep than the distal condyles and quickly shallows to a height of 17.1 mm before reaching the distal condyles. The distal articulation is extensive, with the condyles sweeping through an arc of more than 180°, with a deep groove between the condyles. A prominent dorsal pit and more modest ventral pit at either end of the groove receive the projecting processes of the ungual phalanx (Fig 4D–H). These characteristics are unique to xenarthran manual phalanges and the large size indicates a ground sloth. However, the incomplete nature of the bone and the similarity in certain manual phalanges of late Pleistocene North American ground sloths obscures the identification of the element. Of North American late Pleistocene ground sloths, the manual phalanx 2 of digit IV in *M. jeffersonii* is quite similar to the manual phalanx 2 of digit III in *N. shastensis*.

If OMNH 77904 is a manual digit IV phalanx 2, that element in *Paramylodon harlani* (Harlan's ground sloth) is rudimentary (Stock, 1925). The same element in *Nothrotheriops shastensis* (Shasta ground sloth) is greatly foreshortened with hardly any shaft between the proximal and distal articulations (Stock, 1925). Thus, OMNH 77904 is unlike that of these two sloths and instead resembles the bone of *M. jeffersonii*. On the other hand, if OMNH 77904 is a manual digit III phalanx 2, that element in *P. harlani* is foreshortened with hardly any shaft (Stock, 1925). The same phalanx of *M. jeffersonii* is far more robust with a mediolaterally, much wider shaft (McDonald, 1977). Thus, OMNH 77904 is unlike both of these taxa, and instead it resembles the element in *N. shastensis* (Paula Couto, 1976). Perhaps future ancient DNA analysis could help identify this incomplete bone.

Nothrotheriops shastensis has no late Pleistocene (Rancholabrean) records in the Ozark Highlands and no fossil record in Oklahoma (McDonald and Jefferson, 2008; a previous record of the species in western Oklahoma (Akersten and McDonald, 1991; Smith and Cifelli, 2000) is Irvingtonian, early Pleistocene, and was re-identified as *Nothrotheriops texanus* [McDonald and Jefferson, 2008]). If the Three-Forks Cave sloth were *N. shastensis*, it would represent a huge 980 to 1190 km northeastward or northward extension in its late Pleistocene range from the nearest known localities in New Mexico, USA, and Nuevo León, Mexico (McDonald and Jefferson, 2008). The numerous North American records of Wisconsin glacial age of *M. jeffersonii* were summarized by Hoganson and McDonald (2007). These records included several from the northern Ozark Highland in Missouri but none in the Arkansas or Oklahoma portions of the Ozarks. Thus, the Three-Forks Cave record represents the first occurrence of Jefferson's ground sloth in the southern Ozark Highlands. We assert that the record in Three-Forks Cave is inconsistent and unparsimonious as *N. shastensis*. This assertion is based on the known paleogeographic distribution of that species and its absence in other Ozark Highland late Pleistocene assemblages and caves, and that the fossil instead represents *M. jeffersonii*.

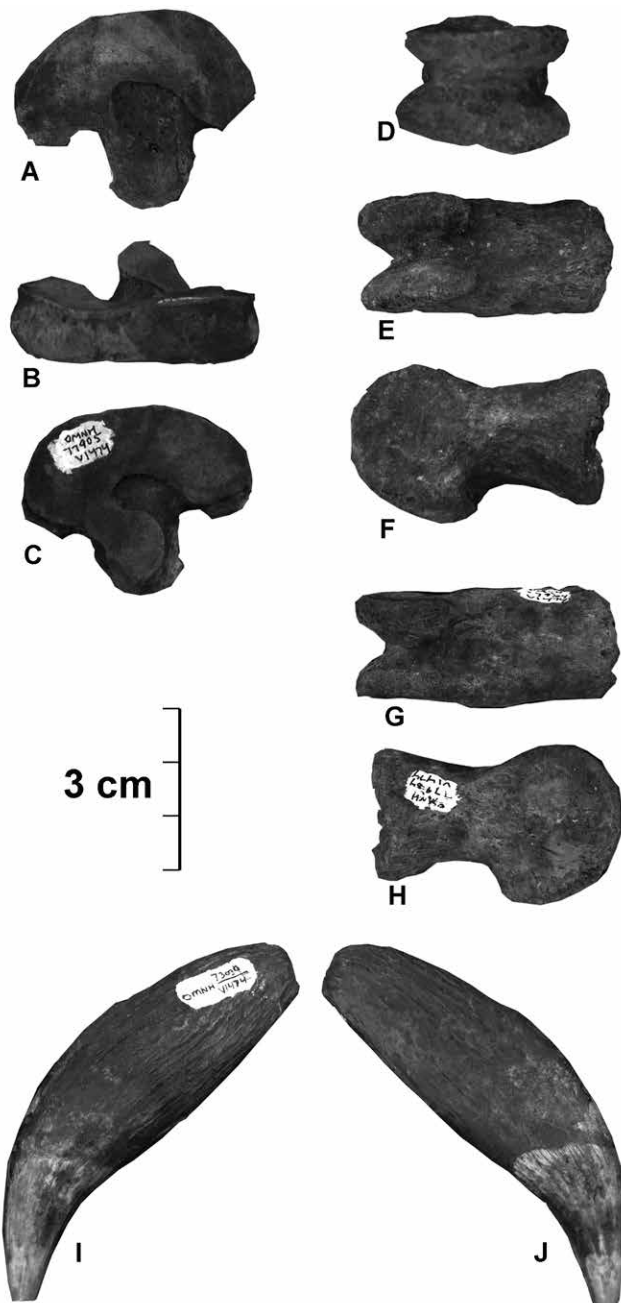


Figure 4. Fossils of large mammals from Three-Forks Cave, Oklahoma. Equidae left lateral ectocuneiform (OMNH 77905) in A, distal view; B, anterior view; C, proximal view. *Megalonyx jeffersonii* phalanx lacking proximal epiphysis (OMNH 77904) in D, distal view; E, palmar view; F, lateral view; G, dorsal view; H, lateral view. *Canis dirus* right upper canine (OMNH 73039) in I, labial view and J, lingual view.

the cave today, but in our paleontological work we noticed no evidence of their use of it as a nursery.

Myotis grisescens (gray myotis)

Material: OMNH 72965, nearly complete cranium in a small piece of carbonate matrix, with left and right P4-M3, missing petrosals (Fig. 5); 72954, rostrum with left M2 and right M2-M3; 72955, rostrum with left P4-M3; 72958, rostrum with both P4-M3; 72960, edentulous rostrum; 77703, right half rostrum with P4-M3; 77704, rostrum with right P4 and M2; 77733, rostrum with left P4; 77734, rostrum with left C1-M3 and right P2-M3; 77735, rostrum with both P4-M3; 77736, rostrum with left P4, M2-M3 and right M2; 77737, rostrum with left P4-M3 and right P4, M2-M3; 77832, left P4; 72956-72957, right dentaries with p4-m3; 78109, left dentary with i2-m2 in a small chunk of matrix; OMNH 72969-72972,

Soricomorpha

Soricidae

Sorex sp. indet. (long-tailed shrews)

Material: OMNH 78524, edentulous right rostrum fragment with alveoli for the entire upper tooth row except for those of the M3 (Fig. 3B), from the Drain.

The alveoli in this skull fragment indicate five unicuspid teeth decreasing in size slightly from front to back, and with the last being distinctly smaller than the others. This condition is seen in several species, including *Sorex arizonae*, *S. cinereus*, *S. haydeni*, *S. lyelli*, *S. merriami*, *S. nanus*, and *S. preblei*; thus, we are unable to assign the specimen to a species.

Chiroptera

Skeletal elements of bats are by far the most common fossils in the Three-Forks Cave deposits, represented by over 840 bones and isolated teeth. All pertain to Vespertilionidae, and most probably belong to *Myotis*, with a few pertaining to other genera. Those elements most diagnostic to the species level are discussed in detail below.

Vespertilionidae

Perimyotis subflavus (tricolored bat)

Material: OMNH 77789, left premaxilla-maxilla fragment with P4-M1 (Fig. 3D); 78214, left P4; 77851, left P4; 78516, edentulous left half rostrum; 78321, left M1 or M2; 78324, right M1 or M2; 77712, left dentary fragment with p4-m1; 77765, right maxilla with C1, P4-M1; all from the Drain. OMNH 77695, left dentary with c1-m2 (Fig. 3E) from the Second Parachute Room.

All specimens include teeth showing very little wear and thus represent young adults. We observed living tricolored bats in Three-Forks Cave, but females of this species typically give birth and raise their young outside caves in summers in tree foliage, lichen-bedecked trees, bromeliads, and rock crevices (Carter et al., 1999; Veilleux et al., 2003, 2004; Perry and Thill, 2007; Farrow and Broders, 2011). As a result, the remains of juveniles are not normally found in caves.

Eptesicus fuscus (big brown bat)

Material: OMNH 78038, left dentary fragment with m1-m2; 77705, left half rostrum with i2-M3; 78337, right M1 or M2; 77729, right dentary with erupting p4 and m3; all from the Drain.

The dentary with erupting teeth (OMNH 77729; Fig. 3G) indicates that *E. fuscus* was using the cave as a nursery roost in the late Pleistocene. The species still utilizes

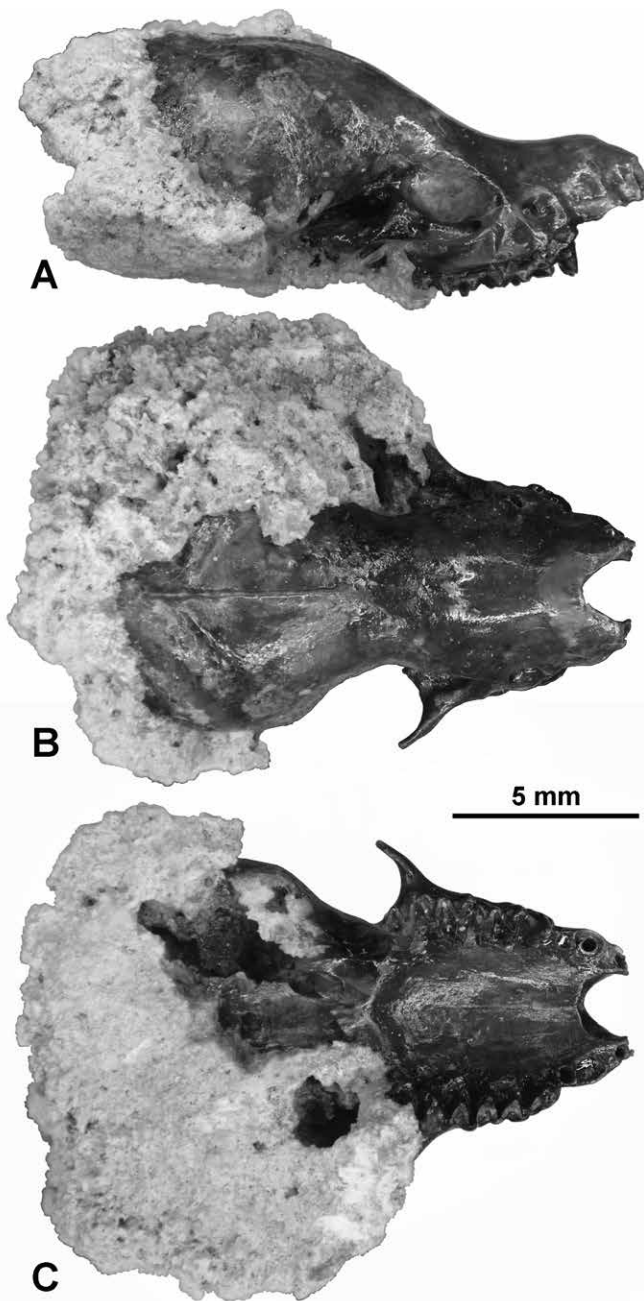


Figure 5. *Myotis grisescens* cranium with adhering matrix (OMNH 72965) in A, lateral view; B, dorsal view; C, palatal view.

heavy tooth wear and indicate aged individuals, whereas relatively few show light to moderate wear. The most complete cranium (OMNH 72965; Fig. 5) and numerous rostra agree closely with modern specimens of *M. grisescens* in morphology and size. The cranium bears a sagittal crest. One rostrum, OMNH 77733, has a less abruptly rising forehead profile than the others, and also has somewhat deeper facial concavities anterior to the orbits and above the infraorbital foramina. It is included here with *M. grisescens* because of a lack of other distinguishing features, but possibly represents a second large species of *Myotis*. Numerous isolated upper molars of bats document a range of sizes, suggesting that more than one species of *Myotis* is present in the assemblage but not represented by any of the more complete specimens. Evidence for this is the relatively small size of several M1s and M2s with transverse widths of 1.5–1.7 mm (e.g., OMNH 77920, 78178, 78179, 78200) compared to those identified as *M. grisescens* with transverse widths of 1.7–2.3 mm. We assigned only our largest specimens to *M. grisescens*, whereas isolated teeth and other elements are assigned to *Myotis* sp. indeterminate.

77747–77748, 77848–77850, complete humeri; OMNH not separately listed by number, numerous elements including juveniles with deciduous and unerupted or erupting permanent teeth (e.g., OMNH 77728, Fig. 3F). All of the specimens, complete enough to be identified as this species, came from the Drain.

We used the key provided by Gaudin et al. (2011) for partial help identifying dentaries of *Myotis* from Three-Forks Cave. *Myotis grisescens* was largest of their Tennessee species of *Myotis* among modern specimens measured. This species has a mandibular length greater than or equal to 11.5 mm whereas *Myotis septentrionalis* and other eastern species have the mandibular length less than 11.4 mm (Gaudin et al., 2011). Of these, their smallest species *Myotis leibii* had an alveolar length (c1-m3) less than or equal to 5.0 mm. Between these size extremes, “No current method can be used to unambiguously identify skeletal remains of the other southeastern US species of *Myotis* to the species level (*M. sodalis*...*M. austroriparius*...and *M. lucifugus*... Therefore, we were unable to distinguish these species in this study” (Gaudin et al., 2011: p. 612).

Of our specimens from Three-Forks Cave referred to the genus *Myotis*, 41 dentaries were measured for species identification using the criteria provided by Gaudin et al. (2011). Summary measurements of this sample were as follows: mandibular length, $n = 18$, observed range = 10.5–14.0, mean = 12.50; mandibular alveolar toothrow length, $n = 41$, observed range = 5.0–8.1, mean = 6.82. The largest of these measurements are consistent with those of Gaudin et al. (2011) to diagnose *Myotis grisescens* and inconsistent with *M. septentrionalis*, while the smallest are equivalent to *M. leibii*. However, some Three-Forks Cave specimens overlap with *M. septentrionalis* and other species. Nine of the large humeri of *Myotis* were complete enough for measurements (Table 1) and all are assigned to *M. grisescens*. Thus, *M. grisescens* is probably present, and additional species of *Myotis* are also likely represented in the sample from Three-Forks Cave, but we cannot identify them with current methods.

Myotis grisescens is the most abundant bat in the Three-Forks Cave sample. Many specimens with erupting permanent teeth indicate use of the cave as a maternity roost in the late Pleistocene. Other specimens exhibit

Table 1. Measurements (mm) of adult, complete fossil humeri referred to the species *Myotis grisescens* from Three-Forks Cave, Oklahoma.

Specimen/OMNH No.	Greatest Length	Proximal Width	Distal Width
72969	24.9	3.7	3.5
72970	24.85	3.45	3.25
72971	24.2	3.5	3.35
72972	25.15	3.45	3.2
77747	26.5	3.65	3.45
77748	24.95	3.5	3.5
77848	24.8	3.7	3.75
77849	25.6	3.55	3.5
77850	24.8	3.5	3.3
77863	26.65	3.75	3.5
77864	26.6	3.8	...
77865	27.05	3.8	3.55
77868	23.75	3.3	3.05
77870	25.3	3.7	3.55
78014	24.9	3.3	3.0
78412	27.85	3.55	3.5
78413	26.5	3.55	3.35
78414	24.5	3.45	3.15
78415	25.4	3.5	2.95
Total number of samples	N = 19,	N = 19,	N = 18,
Mean of samples	Mean = 25.487	Mean = 3.566	Mean = 3.356

Although we did not notice *M. grisescens* using Three-Forks Cave during our paleontological work and no systematic search for them has been done there, the species forms a large maternity colony in another nearby cave on Gittin' Down Mountain (Sasse et al., 2007). They almost certainly also utilize Three-Forks Cave and other caves in the vicinity at times, although we are unaware of their recent use of Three-Forks Cave as a nursery. These bats form part of the historical "Southern Sub-population" of the Ozark population of this endangered species (Sasse et al., 2007).

Carnivora

Canidae

Canis dirus (dire wolf)

Material: OMNH 73039, right upper canine (Fig. 4I, J), from the Drain.

The tooth shows light wear on the tip and a slight wear facet from contact with the lower canine on its anterior face; there are modest

longitudinal ridges running down the mesial and distal surfaces. The complete root is preserved and the pulp cavity is closed, indicating an adult. The crown of the canine measures (APL × TW) 19.7 × 14.1. By comparison, two other C1s of *C. dirus* from localities of Pleistocene age in Oklahoma (at Burnham and Marlow; Cifelli et al., 2002; Czaplewski, 2003) measure 17.1 × 12.1 and 18.7 × 12.1, and a C1 from Pul-103 Cave, Pulaski Co., Missouri measured 17.7 × 12.7 (Hawksley et al., 1963). Upper canines of modern *Canis lupus* are about 2–4 mm smaller in each of these dimensions. Elsewhere in the Ozark Highlands, *C. dirus* is known as a late Pleistocene fossil at 10 localities in Missouri and two in Arkansas (Dundas, 1999).

Vulpini (foxes)

Genus indet.

Material: OMNH 77902, right humerus missing distal end, from the Drain. Measurements of the specimen are proximal articular width, 16.6 mm; midshaft diameter medial-lateral, 7.0 mm; midshaft diameter, anterior-posterior, 9.4 mm.

The humerus is identified as that of a canid based on the lack of an entepicondylar foramen and the presence of a supratrochlear foramen. Its small size further distinguishes it from *Canis* spp. (coyotes and wolves) as one of the foxes (*Vulpes* or *Urocyon*).

Ursidae

Arctodus simus (short-faced bear)

Material: OMNH 73334, partial skeleton from the Second Parachute Room (consisting of small cranial fragments, partial dentary: left c1, lower incisor, right P4, right M1, right maxillary fragment with alveoli for P1 and P2, P2 or P3; portions of ilium, ischium, head of humerus, right humerus distal fragment, portions of femur, cervical vertebrae, thoracic vertebrae, rib fragments, costal ribs and sternbrae, lumbar vertebra, caudal vertebrae). Nine elements are referred to as a second individual because they were collected from a passage west of the Drain (Fig. 2D). These remains are cataloged separately as OMNH 78515, unworn small P/p2 or P/p3; 73040, thoracic vertebra; 73041, partial ulna; 77897, left proximal radius shaft fragment; 77898, navicular; 77896, right proximal tibia with partial articular surface; 77899, metatarsal III; 77900, proximal phalanx; 73042, phalanx.

Measurements of teeth associated with the partial skeleton from the Second Parachute Room are: c1 APL 28.6, TW 19.3; P4 APL 21.6, TW 14.9; M1 APL 24.9, TW 23.1; m2 (from Puckette 1976) APL 29.5, TW 19.5. Measurements of the metatarsal III from the Drain are: greatest length 79.4, greatest proximal width 18.0, greatest proximal depth 24.7,

greatest distal width 18.1. The measurements of the metatarsal III from Three-Forks Cave are smaller than those for two third metatarsals, reported by Merriam and Stock (1925). By comparison with other published measurements, the bears from Three-Forks Cave were both small individuals of *A. simus*.

This species is recognizable by the presence of a deep pre-masseteric fossa in the dentary (Fig. 6G), large size, and cheek teeth morphologically distinct from those of ursine bears. Two individuals of the giant short-faced bear are represented in the faunal assemblage from Three-Forks Cave; parts of each were found in separate rooms (Figs. 2B and 2D) within the cave and show different preservation. One individual, found in a passageway adjacent to the Second Parachute Room (Fig. 2B), is represented by greatly worn teeth and numerous postcranial bones and fragments (OMNH 73334; Figs. 6, 7). The second individual, from a passage near the Drain, comprised a cluster of scattered bones and a little-worn P/p2 or P/p3 (Fig. 8). The former specimen represents associated parts of a senescent individual bear, while the latter cluster of isolated elements represents a younger adult. The former specimen includes a tooth collected years ago and prior to our work in the cave that was previously published by Puckette (1976), conserved in the University of Arkansas Museum (UAM) collection. The specimen from the University of Arkansas consists of a heavily worn m2, UAM catalog number 75-839-1, and was the first record of *A. simus* in Oklahoma. This m2 is almost certainly associated with the elements collected by us from the same, aged individual, because it shows a similar advanced stage of tooth wear and identical preservation. Thus, parts of this individual are preserved in two different collections, in the University of Arkansas and the Oklahoma Museum of Natural History. In general, preservation of the bones and teeth of the first bear was poorer, with the bones being light in color, much broken and abraded, and with extensive rodent-gnawing on some pieces (Fig. 7D, L). Bones of the second bear were dark brown and some pieces had originally been concreted with calcite (visible on the centrum of the thoracic vertebra, Fig. 8E). Because direct association of the several scattered elements of the second individual of *A. simus* could not be demonstrated, these elements were cataloged separately.

Short-faced bears are hypothesized to have been sexually dimorphic, with males larger than females (Kurtén, 1967; Churcher et al., 1993). The two individuals of *A. simus* in Three-Forks Cave are relatively small and, therefore, likely to represent females; this is consistent with the conclusions of Schubert and Kaufmann (2003) that only females denned in caves. We cannot determine whether the bears used the cave for hibernation, birthing young, or denning. Adjacent to Three-Forks Cave is a small, separate cave that was probably once a part of the same cave complex. It contains a crater-like feature about 2 m in diameter that represents a possible short-faced bear bed, and other caves in the area may contain them as well (personal observations). By comparison, recent black bear beds in Three-Forks Cave are

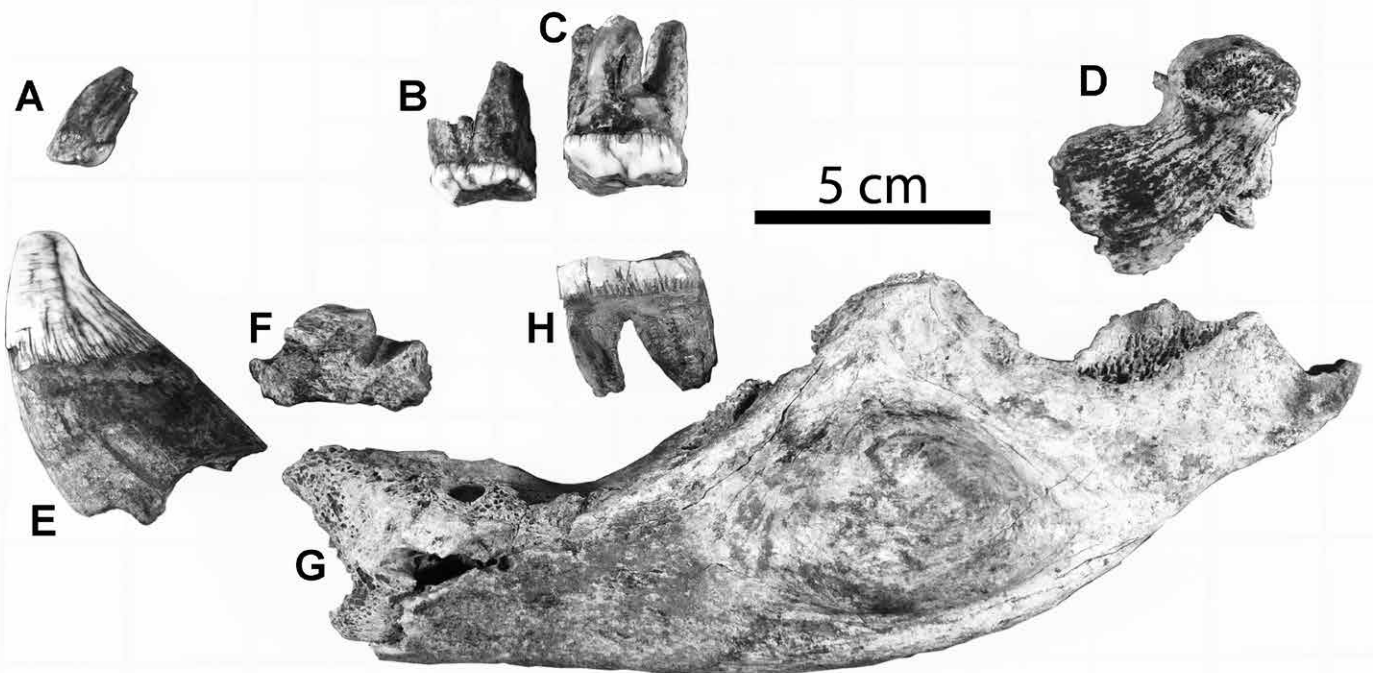


Figure 6. Teeth and dentary fragments of *Arctodus simus* found near the Second Parachute Room in Three-Forks Cave, Oklahoma. All are cataloged as parts of OMNH 73334 except H. A, upper(?) incisor in lateral view; B, right P4 in lingual view; C, left M1 in lingual view; D, medial end of right condyloid process of dentary in medial view; E, left lower(?) canine in labial view; F, small fragment of right dentary with alveoli for p3 and p4; G, broken and abraded left partial dentary with deep ends of some alveoli forward to the canine alveolus, in lateral view; H, right m2 (UAM 75-839-1) in labial view.

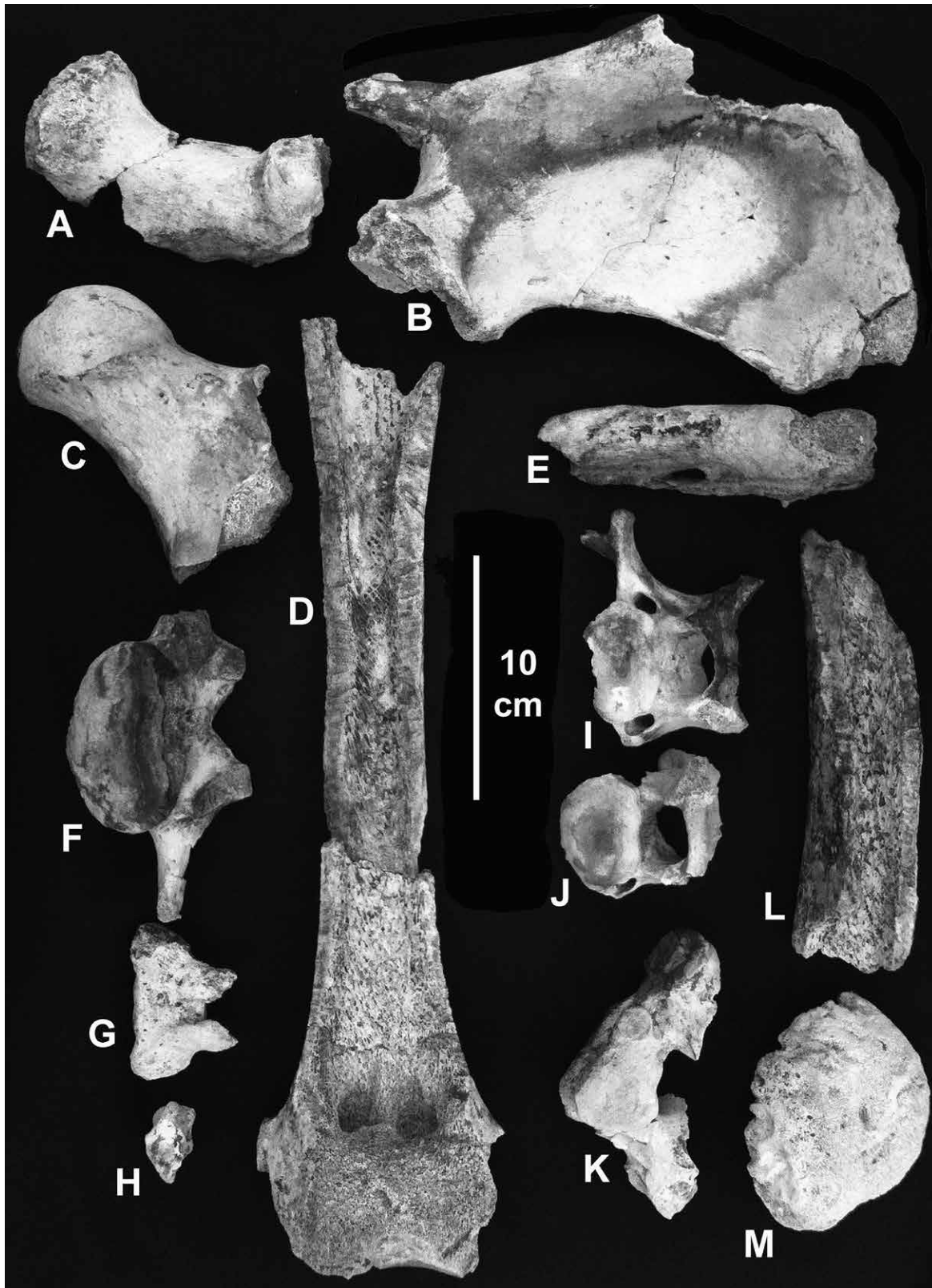


Figure 7. Selected postcranial skeletal elements of *Arctodus simus* (OMNH 73334) found near the Second Parachute Room in Three-Forks Cave, Oklahoma. A, right ischium in lateral view; B, right ilium in lateral view; C, head of femur in anterior view; D, longitudinally split, posterior and distal portion of the left femur in anterior view, with broken edges of shaft extensively gnawed by rodents and distal portion abraded; E, distal fragment of humerus showing entepicondylar foramen in posteromedial view; F, partial lumbar vertebra in posterior view; G, proximal caudal vertebra in dorsal view; H, mid-caudal vertebra in anterior view; I, J, portions of two cervical vertebrae in posterior view; K, partial thoracic vertebra in anterior view; L, shaft fragment of femur showing extensive rodent gnawing; M, right partial head of humerus in proximal view.

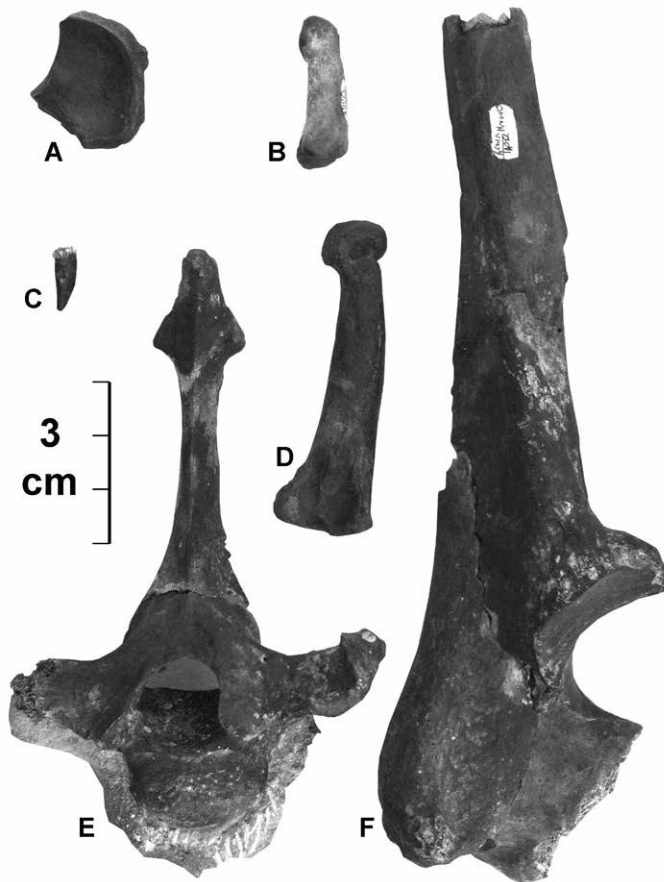


Figure 8. Skeletal elements of *Arctodus simus* found west of the Drain in Three-Forks Cave, Oklahoma. A, left navicular (OMNH 77898) in proximal view; B, phalanx (OMNH 77900) in lateral view; C, little worn P/p2 or P/p3 (OMNH 78515) in lateral view; D, left metatarsal III (OMNH 77899) in lateral view; E, thoracic vertebra (OMNH 73040) in anterior view, with adhering calcite on ventral surfaces; F, right partial proximal ulna (OMNH 73041) in medial view.

Material: OMNH 78523, p4, from the Drain.

The p4 is abraded and polished with all edges rounded, probably from water-wear. Nevertheless, it can be identified as that of *Geomys* in being hypselodont and bilophodont with wide dentine tracts on either side extending the full height of the crown, a narrow connection between the protolophid and metalophid, and V-shaped re-entrant angles (Hall and Kelson, 1959).

Heteromyidae

Chaetodipus or *Perognathus* sp. indet. (pocket mouse)

Material: OMNH 78522, right m1 or m2, from the Drain.

Measurements of the molar are APL, 0.95; TW, 1.35. The cheek tooth is rooted, low-crowned, and bunolophodont with two lophs. It bears three well-developed roots, and its occlusal surface is worn such that the protostylid is confluent with metalophid-protoconid. Its measurements are slightly smaller than m1s and m2s in *Chaetodipus hispidus*, the species of pocket mouse with a modern distribution nearest to the Ozark Highland in Oklahoma (Caire et al. 1989; Kays and Wilson, 2002). A worn, isolated molar such as this lacks apomorphic morphological characteristics to distinguish between the genera *Chaetodipus* and *Perognathus*.

Nevertheless, the pocket mouse specimen, potentially, is biogeographically significant. If it represents a true occurrence in a habitat near the cave, it indicates the extralimital presence of a perognathine in the late Pleistocene of the southwestern Ozark Highlands, where none has occurred in historic times. In modern times, the mouse *Chaetodipus hispidus* has only been found west of the Neosho-Arkansas Rivers that delimit the western edge of the Ozark Highland in Oklahoma. The species has been recorded as near as 70–90 km west of Three-Forks Cave just west of the Ozark

about 1–1.5 m across (personal observation). The potential short-faced bear beds deserve further investigation.

As noted in the Introduction, the *A. simus* tooth UAM 75-839-1 from Three-Forks Cave was included by Schubert (2010) in his review of North American records of giant short-faced bears, and he also provided a tentative radiometric date of 33,143 to 34,983 ybp for the specimen. This remains the only available age estimate for the vertebrate faunal assemblage of Three-Forks Cave. Elsewhere in the Ozark Highlands, *A. simus* has been found in seven other localities in Missouri (Richards et al., 1996; Schubert and Kaufmann, 2003).

Perissodactyla

Equidae

Equus or *Haringtonhippus* sp. indet. (extinct horse)

Material: OMNH 77905, left ectocuneiform (Fig. 4A–C), from a passage near the Second Parachute Room.

This ankle element is the only identifiable horse bone recovered from the cave. It is not diagnostic to the generic level because late Pleistocene North American horses were recently separated into two genera, *Equus* and *Haringtonhippus* (stout-legged and stilt-legged horses, respectively), that are morphologically distinguishable only by their proximal foot bones (metacarpals and metatarsals) (Heintzman et al., 2017), which were not found in Three-Forks Cave. Measurements of the ectocuneiform from Three-Forks Cave are: greatest medial-to-lateral width, 43.6 mm; least anterior depth, 8.9 mm. Horses were widespread throughout the Ozark Highlands in the late Pleistocene, as evidenced by their occurrence in at least nine localities (FAUNMAP Working Group, 1994; <http://www.ucmp.berkeley.edu/faunmap/about/index.html>).

Rodentia

Geomyidae

Geomys sp. indet. (plains pocket gopher)

Highland (Caire et al., 1989). The species' modern habitat preference suggests an extension of relatively dry, grassy or open plains habitat into the Ozarks during the late Pleistocene. However, the pocket mouse fossil might represent the remains of a prey species brought into the cave from a more distant habitat by a predator such as an owl. Owls can transport prey animals they have ingested for some distance until later egesting a pellet. This phenomenon and the distance involved appears to have received little attention in taphonomic studies of owl pellet accumulations (Andrews, 1990; Walton, 1990; Terry, 2004; Czaplewski, 2011). If an owl moves a great distance in between ingestion and egestion, such as during a migration or a less distant hunting bout, it could potentially accumulate prey from habitats far from the locality where it casts a pellet containing the prey remains. The presence of a great horned owl fossil bone in Three-Forks Cave heightens the possibility, but the owl bone does not demonstrate, that the pocket mouse fossil is an intrusive member of the paleo assemblage of the cave (Andrews, 1990). The species *Chaetodipus* cf. *hispidus* was previously recorded in the Ozark Highlands at Crankshaft Cave, Missouri, in the Wisconsinian glacial period (Parmalee et al., 1969; FAUNMAP Working Group, 1994).

Cricetidae

Peromyscini

Peromyscus, *Ochrotomys*, or *Podomys* sp. indet. (mouse)

Material: OMNH 77861, left m1; 78525–78526, left M1s; 78527, right M3; 77701–77702, right dentaries with i1; 73038, edentulous maxilla; all from the Drain. OMNH 77699, dentary with i1, from the Second Parachute Room.

Measurements of the molars (APL × TW) are: 77861, 1.50 × 0.95; 78525, 1.85 × 1.10; 78526, 1.80 × 1.10; 78527, 0.95 × 0.90.

The specimens have small, rooted, cusped, bunodont teeth typical of deer mice and their relatives (Osgood, 1909; Bradley et al., 2007). Based on the paucity of material and the possibility that several different, but morphologically similar, species of *Peromyscus* and closely-related genera occurred in the vicinity of Three-Forks Cave, it is not possible to refer these few specimens to a genus.

Neotoma cf. *floridana* (eastern woodrat)

Material: OMNH 77700, left dentary fragment with m1-m3; 78550, left calcaneum; 73019, proximal ulna; 77922, femur; all from the Drain.

The molar teeth are rooted, hypsodont, lophodont and semi-prismatic, which are typical of woodrats that commonly utilize caves and rock shelters across North America (Vaughan et al., 2015). The bilophate m3 is characteristic of species in the subgenus *Neotoma* and the m1 has essentially no anterior lateral dentine tract, consistent with *N. floridana* (Harris, 2014). The teeth and bones represent a large woodrat the size of recent *N. floridana* (Fig. 3H). In addition to the body fossils, several coprolites (OMNH 78551, 78546) from the Drain are similar to scats of *Neotoma* and probably are attributable to woodrats dwelling in and near the cave in the late Pleistocene. The original scat contents have been replaced by sediment grains, but the contents retain the shape of *Neotoma* scat pellets as are seen in numerous caves throughout North America.

Arvicolinae

Microtus cf. *ochrogaster* (prairie vole)

Material: OMNH 78353, right dentary fragment with m1 (Fig. 3C), from the Drain.

The m1 is hypselodont, with prismatic crown pattern, and bears cementum in the re-entrant angles, characteristic of voles of the genus *Microtus* (Semken and Wallace, 2002). The crown pattern shows three closed triangles, an anteriorly-rounded anterior loop, and low dentine tracts, typical of the subgenera *Pitymys* and *Pedomys*. Enamel is thicker on the forward edges of triangles relative to the rearward edges; the medial portions of the re-entrant angles curve forward or not at all; and the sixth re-entrant angle is shallow. These features are characteristic of *Microtus* (*Pedomys*) *ochrogaster*, but the specimen is only tentatively referred to that species because of variability and overlap of some characteristics with *M. (Pitymys) pinetorum* (Semken and Wallace, 2002).

Lagomorpha

Leporidae

Sylvilagus sp. indet. (cottontail rabbit)

Material: OMNH 77732, left p3; 78552, right fifth metatarsal V; 78554, phalanx; from the Drain.

The p3 measures 2.8 mm APL × 2.7 mm TW, is hypselodont, heavily invested with cementum anteriorly, labially, and within the re-entrant angles, and has enamel that varies greatly in thickness across the occlusal surface. It shares with *Sylvilagus* the normal anterior, anteroexternal, and posteroexternal re-entrant angles, as well as weak crenulations of the enamel, including that on the walls of the posteroexternal re-entrant (Hibbard, 1963), but the material lacks species-level diagnostic characters.

Discussion

Other than four extinct large mammals, none of the vertebrates from Three-Forks Cave became extinct at the end of the Pleistocene. In Three-Forks Cave, these extinct megafaunal members include the ground sloth *Megalonyx jeffersonii*, the short-faced bear *Arctodus simus*, the dire wolf *Canis dirus*, and a horse, family Equidae; indicating a Rancholabrean age for the assemblage. All other taxa, as far as they are identifiable, still occur in the Ozark Highlands today except for one, a pocket mouse of the subfamily Perognathinae, genus *Chaetodipus* or *Perognathus*. The pocket mouse suggests either the extralimital occurrence of this mouse in the southwestern Ozark Highlands during the late Pleistocene--and thus a potential extension of relatively dry, grassy or open habitat into the Ozarks--or else it represents the remains of a prey species brought into the cave from a more distant habitat by a predator such as an owl, and, thus, is intrusive. In historic times, the mouse *Chaetodipus hispidus* has been found as near to Three-Forks Cave in several of the Oklahoma counties immediately west of the edge of the Ozark Highland (Caire et al., 1989). The total of 23 vertebrate taxa in the fauna from Three-Forks Cave makes it the largest known vertebrate assemblage from a cave in the Ozark Highland of Oklahoma, exceeding nearby Sassafras Cave with an assemblage of nine taxa (Czaplewski et al., 2002). Two of the taxa provide the first records of their respective species in the late Pleistocene of Oklahoma, the freshwater drum (*Aplodinotus cf. grunniens*) and great horned owl (*Bubo virginianus*).

Among the bat bones, numerous specimens, especially of *Myotis grisescens*, consisting of jaws and jaw fragments with deciduous teeth, erupting teeth, and enamel caps of upper and lower molars from juveniles (Fig. 3F, G) were recovered. Similarly, less common remains of *Eptesicus fuscus*, with erupting permanent teeth, occurred in the cave deposits. The fossils of immature individuals indicate the use of Three-Forks Cave as a maternity roost for these two species. Other than the juveniles, specimens of *M. grisescens* include fossils showing stages of tooth wear from slight to heavy, indicating at least some aged adult bats. Of the few bat specimens that could be identified as *Perimyotis subflavus*, all pertained to young adults with little-worn teeth. All three species of bats found as fossils still occur in Three-Forks Cave today; we also observed *Corynorhinus townsendii ingens*, the endangered Ozark big-eared bat, in the cave. However, we found no fossils of that species. The fossils indicate that environmental conditions of temperature and humidity, suitable for birthing young bats within Three-Forks Cave in the late Pleistocene, were not so different from today.

Two individuals of the short-faced bear, *Arctodus simus*, occurred in Three-Forks Cave, as determined by their discovery in two separate parts of the cave, different bone preservation, and different stages of tooth wear, with one having greatly worn teeth and the other preserving a single, lightly worn tooth. Both individuals are relatively small, possibly indicating they were females of this potentially sexually-dimorphic species (Schubert and Kaufmann, 2003). As noted above, several of the bone fragments of *A. simus* are extensively rodent-gnawed, possibly by woodrats living in the cave; their scats were also preserved. Woodrats might also have been responsible for collecting some of the bones in the cave deposits. The owl *Bubo virginianus* probably contributed to the accumulation of small vertebrate remains. Short-faced bears are thought to have been carnivorous-omnivorous and are implicated as scavengers of large mammal carcasses (Matheus, 1995, 2003; Sorkin, 2006; Figueirido et al., 2010, 2017). Short-faced bears and dire wolves using the cave are additional potential sources of the remains of large mammals (horse, ground sloth), and possibly also of smaller mammals like the fox (*Vulpini*), brought in as prey remains or scavenged body parts. Large depressions in Three-Forks Cave and other nearby caves resemble beds of denning black bears, except for the much larger size of some, suggesting they could be beds of short-faced bears.

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