

A PLEISTOCENE TAPIR AND ASSOCIATED MAMMALS FROM THE SOUTHWESTERN OZARK HIGHLAND

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*A mud deposit in Sassafras Cave near Stilwell, Oklahoma, produced a small assemblage of fossil vertebrates including an unidentified salamander and the mammals *Myotis* sp., *Lasionycteris noctivagans*, *Pipistrellus subflavus*, *Tamias striatus*, *Peromyscus* sp., *Reithrodontomys* sp., *Microtus* sp., and *Tapirus veroensis*. The fossiliferous mud deposit is a stream terrace containing abundant red clay accumulated behind roof fall and breakdown boulders that temporarily dammed the main stream-passage of the cave. The tapir fossils indicate a late Rancholabrean (late Pleistocene) age for the deposit. This is the first report of a tapir from the Oklahoma Ozark Highland and only the second report of Pleistocene megafauna from a cave in eastern Oklahoma. The tapir is represented by a partial skeleton with some of the distal leg bones articulated in life position in the deposit. The animal probably died while it was standing or lying in the mud, possibly after falling into the cave or walking in through an entrance that had a different configuration in the Pleistocene than the present sinkhole entrance.*

The Ozark Highland is an old remnant of a dissected plateau in southern Missouri, northern Arkansas, and northeastern Oklahoma. Today, much of the area is covered by steep-sided hills with intervening valleys cut by many clear streams that originate in the higher elevations. Numerous limestone caves occur throughout the Ozark Highlands, most of which in Oklahoma have developed within rocks of lower Pennsylvanian (Hale Formation) or Mississippian (Pitkin Formation, Keokuk Formation, or St. Joe Group) age. Sassafras Cave is one of seven known caves that occur in a point of a hill in central Adair County. The point has an area of ~20 hectares and is underlain by the Hale Formation in which the caves formed. Most of the caves were probably connected at one time but are currently separated by breakdown, clastic fills, or erosion. The total combined length of the known caves is over 4 km.

Sassafras Cave (OMNH locality V566), Adair County, Oklahoma, is at the southwestern edge of the Ozark Highland. The mapped length of the cave is 365 m (Fig. 1). The passages average 2 m wide and 6 m high. Cavers dug open the present entrance, a 10-m-deep sinkhole, in 1969-1970 while searching for new caves. However, chert flakes (cultural materials from pre-Columbian Indians) found inside the cave indicated that there was a prehistoric entrance in the vicinity of the present entrance. The cave, on the property of the NSS Donald R. Russell Cave Preserve, was donated for purposes of research and preservation.

In 2001, one of the authors (CR) and Sylvia Russell collected parts of a fossil tapir skeleton in a mud bank on the floor of a main passage in Sassafras Cave (Fig. 1). The mudbank is a remnant deposit of unconsolidated sediments that possibly accumulated in an ephemeral subterranean pond behind a pile



Figure 1. Location map and plan view of Sassafras Cave, showing discovery site of tapir skeleton in a Pleistocene terrace. NSS standard map symbols follow Hedges *et al.* (1979). Ceiling heights (encircled numbers) are given in feet.

of breakdown boulders that presently occupies the passage, forming a dam. Today, this pile of boulders rises 2.2 m above the floor of the passage on the downstream side of the dam. The fossiliferous deposit, no greater than 30 m long and 3 m wide, occupies a short, roughly linear section of cave passage. The greatest depth of the deposit is undetermined but is probably not more than 2 m. Based on core samples we made (by pushing in PVC pipe by hand or with a sledge hammer), the sediments had accumulated behind the dam to a depth of at least 1.6 m upon the limestone bedrock (Fig. 2). Apparently the breakdown dam was later breached and the stream in the cave

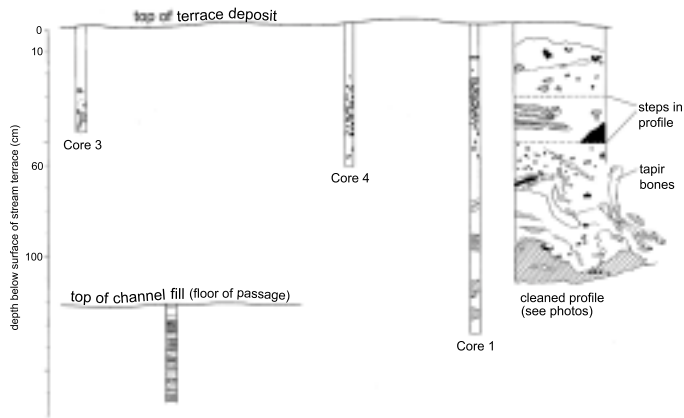


Figure 2. Diagram of cleaned profile and cores showing stratigraphy in a Pleistocene stream terrace and a more recent stream deposit in Sassafras Cave, Oklahoma. Lateral distance is foreshortened to save space; actual distance from Core 3 to Core 1 was ~25 m. Hatching indicates red clay. In Core 2, black indicates organic layer; in the other cores and profile black indicates rocks. The profile was cut adjacent to the spot where the articulated left lower leg bones of the tapir were found. As shown by the cleaned profile and cores 1, 3, and 4, essentially the entire terrace deposit consists of sandy clays.

incised these sediments, leaving a very short (2-m-long) remnant mudbank along the base of the south wall immediately upstream from the breakdown dam, and a much longer (12-m-long) terrace along the base of the north wall that begins 17 m from the dam.

The terrace forms a firm ledge along the north wall of the passage where the tapir skeleton was found. Stratification is visible where we cut profiles in the terrace deposit adjacent to the tapir skeleton (Figs. 2 & 3). The unit in which the tapir skeleton occurred is composed primarily of red brown, yellow brown, and dark brown sandy clay interspersed with structureless blebs of bright red clay that become more frequent in the deeper part. Dispersed through the deposit are occasional cobbles and pebbles of weathered limestone and shale originating from the cave walls and ceiling, as well as a few isolated Paleozoic invertebrate and vertebrate fossils. The deeply weathered shale cobbles within the mud were unconsolidated to poorly consolidated when wet and very friable. The Paleozoic invertebrates are tiny snails (Mollusca: Gastropoda) and columnal ossicles of crinoid stalks (Echinodermata: Crinoidea); the vertebrate remains are tiny shark teeth of several types (Chondrichthyes; W. May 2001, pers. comm.). These Paleozoic fossils entered the Pleistocene deposit as residue weathered from the surrounding limestone. The tapir skeleton and other vertebrate bones occurred in the upstream (east) end of the north terrace about 27 m from the dam. Subsequent further collecting in the deposit yielded more bones of the tapir, and screenwashing of the encasing mud produced—in addition to the Paleozoic animal fossils—the



Figure 3. Photograph of profile cut into the mud deposit in which the fossils occurred. This is the same profile as shown in Figure 2. The hind leg and foot bones of the tapir occurred in the area at the lower right in this photograph (below the person and immediately to the right side of the bottom of the cleaned profile). The photo was taken after the tapir bones were removed.

remains of a few small vertebrates including bats and rodents.

Color and texture of the muds in which the tapir was preserved were field-judged under wet conditions (as the samples were taken from the cave) in order to assess the relative proportions of sand, silt, and clay particles. Donald G. Wyckoff did the field-judging in the lab at the Oklahoma Museum of Natural History (OMNH). The mud encasing the tapir's foot bones appeared in a profile cut to be a weakly stratified, possibly bioturbated unit of sandy clay that was very sticky, mottled red and yellowish red when wet (2.5YR 4/8 and 5YR 4/6; Munsell Soil Color Charts, 1998 revised edition, New Windsor, New York). This unit also contained frequent blebs and chunks of fine red clay (2.5YR 4/6). Immediately adjacent to the bright red clay around the left hind foot skeleton was a "stringer" of manganese oxide. This stringer was a thin sedimentary feature that swept around the front and sides of the tapir's left foot skeleton, sub-parallel to the contour of the foot and between the red and mottled red, yellowish red, and brown

muds. The bacterial decay of animal flesh sometimes leaves behind manganese oxides (B. Schubert 2001, pers. comm.). There was a small void (air space) in the mud over the top of the metatarsals of the left foot. Above the red and yellowish red mud on top of the left hind foot was a small mass of stratified dark brown mud (clay fine sand; 7.5YR 3/3 when wet) that appeared grayish in caving headlights. This stratified dark brown mud contained a bat radius. Other than these *in situ* deposits, much of the surrounding deposit from which other fossils were recovered consisted of variegated red, yellowish red, and brown muds that were disturbed by foot traffic in the cave and by efforts to recover the fossils. In places, these disturbed muds also contained flat, subangular pebbles derived from the country rock making up the cave walls.

The red clay that forms a major component of the terrace deposit in Sassafras Cave is a common feature of cave sediments throughout the Ozark Highland (Bretz 1942; Jennings 1985; Brod 1999; Reams, no date). Brod (1999) reported that no sediment information—especially on the red clay—was available for Oklahoma caves, but the occurrence of red clay there is expected because of its widespread occurrence in Missouri and Arkansas Ozark caves. In Sassafras Cave, the red clay blebs might not be in their primary depositional context in the muds in which the tapir bones occurred, but they clearly were present when the tapir died in the late Pleistocene. These Ozark red clays consist of very fine quartz particles, clay minerals (kaolinite and illite), and iron minerals that give them their red color (Brod 1999). The clay was primarily derived from surface weathering and was originally emplaced in Ozark caves probably under phreatic conditions during cave development (Brod 1999).

Clay minerals such as kaolinite are important to herbivorous mammals because the clays are ideal for adsorbing many kinds of biochemical toxins produced by the plants they eat (Barlow 2000). Tapirs and many other herbivorous vertebrates eat clay-rich soils, a behavior known as geophagy (Barlow 2000). The clay deactivates the toxins in foliage and other plant tissues. In a predominantly limestone region such as much of the Ozark Highland, clay minerals may not have been widely available to geophagous megaherbivores. It is feasible that tapirs were attracted to Ozark caves such as Sassafras Cave as a source of clay for detoxifying their intestines.

A 44-cm core taken from the center of the passage in the bed of the stream cut between the north and south terraces did not reach bedrock. It revealed a very different column from the terrace and was comprised entirely of thinly layered, unconsolidated, cross-bedded sands and silty sands (Fig. 2, core no. 2) that represent an active channel or cut-and-fill deposit, probably of Holocene age.

A small sample of the well-preserved tapir bone was sent to Beta Analytic, Miami, Florida, for AMS dating. Unfortunately, the bone did not yield a reliable collagen fraction for dating the time of death of the tapir. All its collagen appeared to have been replaced or removed, and it contained only organic molecules probably from the soil and/or humus that invaded the

bone after its burial (R.E. Hatfield 2001, pers. comm.). Thus, the numerical age of the bone could not be determined.

SYSTEMATIC PALEONTOLOGY

Class Amphibia

Order Caudata (salamanders)

Family indeterminate

Material.—OMNH 70976, caudal vertebra.

Discussion.—This vertebra measures 2.5 mm in centrum length. It is somewhat abraded (stream-worn?) and the hemal arch and delicate processes are broken. It bears an ossified cap on the anterior cotyle, forming a small condyle; in temperate North America, this condition is typical of members of the family Salamandridae (newts) and is known to occur in a few species of Plethodontidae (lungless salamanders) (Holman 1995; Hulbert 2001). The Sassafras Cave specimen probably pertains to one of these two families, but a caudal vertebra is insufficient for a familial identification.

Class Mammalia

Order Chiroptera

Family Vespertilionidae

Myotis sp. indeterminate

Material.—OMNH 59520, edentulous left dentary fragment with root of p3 and alveoli for all teeth except the incisors; OMNH 70972, right premaxilla with I1-I2; OMNH 70971, right maxilla and premaxilla fragment with I1-P4; OMNH 70961, left half of rostrum with C1-M3; OMNH 70970, right maxilla with P3-M3; OMNH 70968, left maxilla with P2 and P4-M3; OMNH 70969, left maxilla fragment with M2-M3; OMNH 70973, right maxilla fragment with P2-P4; OMNH 70966, right dentary with p4-m3; OMNH 70967, left dentary with i1-m3; OMNH 70965, right dentary with p4-m3; OMNH 70964, right dentary with p3-m3; OMNH 70974, left dentary with p3-p4 and m2; OMNH 70975, left dentary fragment with p2-p4; OMNH 59519, left proximal humerus; OMNH 70962, right distal humerus; OMNH 70963, right distal humerus.

Discussion.—Five species of *Myotis* (*M. grisescens*, *M. leibii*, *M. lucifugus*, *M. septentrionalis*, and *M. sodalis*) occur in the modern fauna of the Ozark Highland. Of these, we compared the Sassafras Cave fossils with skulls and humeri of all species except *M. leibii*, for which no comparative skeletons were available, and *M. septentrionalis*, for which skulls but no postcranial materials were available. We used one or two skulls and humeri each of *M. grisescens*, *M. lucifugus*, and *M. sodalis*, as well as a skull and humerus of *M. austroriparius*. The last species does not occur today in the Ozark Highlands but does occur to the south in southeastern Oklahoma. We also compared dental measurements of the fragmentary fossils with those of our comparative specimens and with numerous standard measurements provided by Miller and Allen (1928). In lieu of comparative specimens of *M. leibii*, we judged the specimens against the measurements provided by van Zyll de Jong (1984).

The various rostral and mandibular fragments preserve different portions of the upper and lower tooth rows. Different species of *Myotis* greatly resemble one another morphologically, making the identification of fragmentary fossils extremely difficult or impossible. Not all Sassafras Cave specimens were complete enough to yield standard measurements that could potentially be useful for determining the species to which the skull and jaw fragments belonged. However, the fossils are consistent with one another in their morphology and appear to represent a single species. The measurements indicate a medium-sized to small species of *Myotis* (Tables 1 & 2) in the size range of *M. lucifugus* and *M. leibii*, and also broadly over-

Table 1. Measurements (to the nearest 0.05 mm) of the upper tooth rows of Pleistocene *Myotis* from Sassafras Cave, Oklahoma, and several Recent species of *Myotis*.

specimen	length of maxillary tooth row (C1-M3)	length of P4-M3
Fossils		
OMNH 70961	5.10	3.75
OMNH 70970		4.00
OMNH 70968		3.95
Modern comparative specimens		
<i>Myotis septentrionalis</i> ¹	6.10	4
<i>Myotis lucifugus</i>	5.2	
<i>Myotis grisescens</i>	5.9	
<i>Myotis austroriparius</i>	5.20	3
<i>Myotis sodalis</i>	5.4	
<i>Myotis leibii</i> ²	5.0	

¹ Means of 2 specimens.

² Means of 32 specimens (from van Zyll de Jong 1984).

lapping but less well-centered within the size ranges of *M. sodalis* and *M. austroriparius*. The measurements of the fossils definitely represent a bat smaller than *M. grisescens* and *M. septentrionalis*. Few salient details of dental morphology exist that are helpful in distinguishing among the eastern US species of *Myotis*. One such feature is

Table 2. Measurements (to the nearest 0.05 mm) of the lower jaws of Pleistocene *Myotis* from Sassafras Cave, Oklahoma, and several Recent species of *Myotis*. Dash indicates broken specimen on which measurement could not be made.

specimen	length of p4-m3	length of m1-m3	alveolar length of c1-m3	length of dentary	height of coronoid
Fossils					
OMNH 70966	4.10	3.50	5.55	10.30	3.15
OMNH 70967	4.15	3.55	5.45	—	—
OMNH 70965	3.80	3.20	—	—	—
OMNH 70964	4.00	3.40	—	—	—
OMNH 70974	4.10	3.20	5.35	—	—
Modern comparative specimens					
<i>Myotis septentrionalis</i> ¹	4.50	3.65	6.40	10.82	3.17
<i>Myotis lucifugus</i>	4.20	3.55	5.80	10.40	2.95
<i>Myotis grisescens</i>	4.70	3.95	6.25	11.90	3.25
<i>Myotis austroriparius</i>	4.00	3.35	5.40	10.20	2.80
<i>Myotis sodalis</i>	4.20	3.50	5.55	10.40	2.80
<i>Myotis leibii</i> ²					2.79

¹ Means of 2 specimens.

² Mean of 32 specimens (from van Zyll de Jong 1984, who did not make the other lower jaw measurements used here).

a weak lingual cingulum on the upper molars that disappears completely around the base of the protocone. This type of lingual cingulum is present in the Sassafras Cave *Myotis* and in the upper molars of all modern species with which we made comparisons except *M. septentrionalis*. *Myotis septentrionalis* has M1-M3 with strong lingual cingula that continue all the way around the bases of the protocones of these molars.

Like the jaw fragments and teeth, the Sassafras Cave humerus fragments are morphologically indistinguishable from those of several species of *Myotis*. Measurements of the two distal humerus fragments are: width of distal articular surface (from lateral ridge of capitulum to medial edge of trochlea), 2.15 mm and 2.10 mm; greatest width of distal humerus, 2.80 mm and 2.83 mm, respectively. In size, the distal humeri most closely match those of *M. lucifugus* and *M. austroriparius*; they are smaller than one specimen of *M. grisescens* and slightly larger than two of *M. sodalis*. Nevertheless, these small samples do not represent the variability in the species. The morphology of the distal humerus is virtually identical in all the species of *Myotis* examined. Therefore, this element is of no help in distinguishing them, and it is not possible to determine the species to which the Sassafras Cave fragments belong based on the fossils presently available.

The toothless lower jawbone (OMNH 59520) has alveoli for a single-rooted p2 and p3, and a double-rooted p4. Only three genera of bats in the USA, *Myotis*, *Corynorhinus*, and *Lasionycteris*, have this lower alveolar formula. OMNH 59520 matches the morphology of *Myotis* and *Corynorhinus* most closely. It is smaller than the dentary of *Lasionycteris* discussed below, and further differs from *Lasionycteris* in having a lateral mental foramen that opens on the side of the dentary between the roots of the canine and p2 instead of between the roots of p2 and p3. The jawbone appears to be less sinuous in dorsal view than in *Corynorhinus*.

In summary, our size and shape comparisons of rostral fragments, jaws, and teeth indicate that the Sassafras Cave *Myotis* is most similar to *M. lucifugus*, *M. sodalis*, and *M. austroriparius*. The fossils definitely do not represent *M. grisescens* or *M. septentrionalis*. We cannot distinguish further among these species based on the sample of fossils that is presently available.

Lasionycteris noctivagans
(silver-haired bat)

Material.—OMNH 59526, right dentary with c1-p2 and m1-3; OMNH 59527, left dentary fragment with p2-m2 (crown of c1 broken) and alveoli for other teeth (Fig. 4A).

Discussion.—These two jaws were found separately by screenwashing but show similar degrees of tooth wear and similar preservation; they may represent the two sides of the mandible of a single bat.

Morphologically, these jaws are virtually identical to those of modern specimens of *L. noctivagans*. In occlusal outline, p2 and

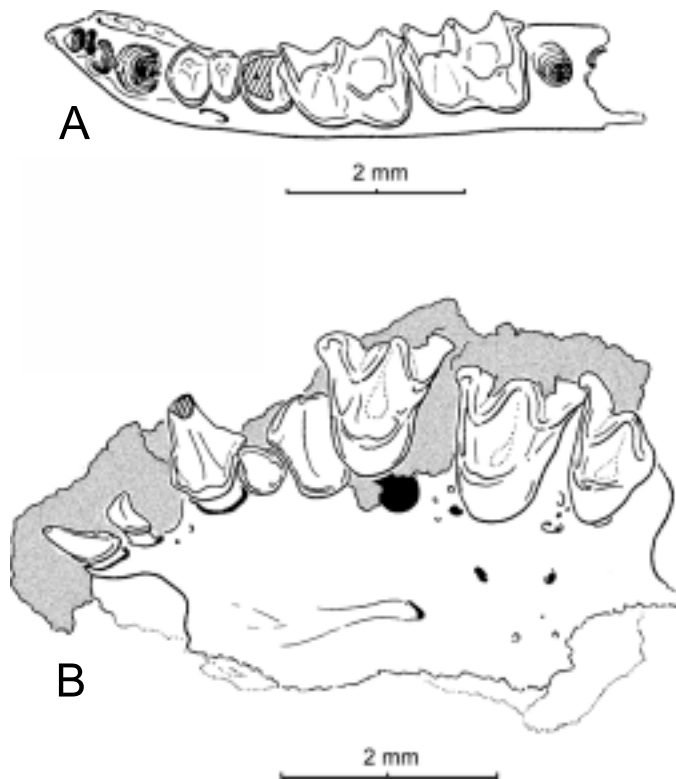


Figure 4. Fossil remains of bats found in association with *Tapirus veroensis* in Sassafras Cave, Oklahoma. **A**, *Lasionycteris noctivagans*, OMNH 59527, left dentary fragment with p2-m2 in occlusal view; **B**, *Pipistrellus subflavus*, OMNH 59523, left half of rostrum with all upper teeth in occlusal view. Hatching indicates breakage; shading in **B** indicates adhering concretion.

p3 are transversely wider than their anteroposterior length, so that these teeth appear anteroposteriorly compressed. This condition differs from *Myotis* in which the width and length are subequal in both p2 and p3. In the fossils and in modern *L. noctivagans*, the occlusal outline of p4 is very short—about as wide as it is long—and appears rather trigonal. This contrasts with *Myotis*, in which all North American species have a p4 that is longer than wide and rather rectangular in occlusal outline. *Corynorhinus* species also have a short p4, but this tooth in *Corynorhinus* has a prominent anterolingual cusp that is absent in the fossil, as well as a relatively straight lingual margin in contrast to the rounded margin in the single p4 available in the fossils. The molar teeth in the fossil also have cusps that are more robust than the distinctively slender cusps and ridges seen in *Corynorhinus*, and the m1 has a much straighter lingual outline in occlusal view than in *Corynorhinus*, which has a strong bend in m1 along the lingual border between the bases of the metaconid and paraconid. The fossils have a lateral mental foramen located between the roots of p2 and p3. In modern specimens of *L. noctivagans*, the lateral mental foramen is situated between the roots of p2 and p3 or is below the canine. By contrast, in *Myotis* the lateral mental foramen opens between the roots of c1 and p2.

Lasionycteris noctivagans has a poor fossil record. The species was previously known from only four localities as a Quaternary fossil or subfossil. These localities are Bell Cave, Wyoming (Zeimens & Walker 1974), Little Box Elder Cave, Wyoming (Anderson 1968),

Upper Sloth Cave, Texas (Logan & Black 1979), and a cave in the Sylamore Ranger District in Ozark National Forest, Arkansas (Saughey *et al.* 1978). Although all these records are from caves, in modern times the species rarely enters caves, preferring to roost in trees. This is the first fossil record of the silver-haired bat in Oklahoma.

Pipistrellus subflavus (eastern pipistrelle)

Material.—OMNH 59523, left half of rostrum with I1-M3 (Fig. 4B).

Discussion.—*Pipistrellus subflavus*, the eastern pipistrelle, is a common and widespread bat across much of the eastern half of the United States and eastern Mexico. It occurs from southeastern Canada to Honduras in a very wide variety of habitat types (Fujita & Kunz 1984). The western and northern limits of its modern distribution are defined by areas lacking caves. In addition, the present northern limit of the species is approximately coincident with the Pleistocene southern limit of the Wisconsinan glaciation; north of this limit, riparian foraging habitat is unsuitable for pipistrelles (Brack & Mumford 1984). *Pipistrellus subflavus* is probably the most common bat in the Ozark Highlands, at least in caves in which it hibernates (Sealander & Young 1955). The species also roosts in trees and other situations outside caves, particularly in the summertime. It occurs in Sassafras Cave in the present day.

Pipistrellus subflavus occurs as a Quaternary fossil or subfossil in at least 31 cave sites scattered across 11 states in the eastern United States. The Sassafras Cave occurrence is the first record of *P. subflavus* as a fossil in Oklahoma and only the second fossil record for the species in the Ozark Highland. The other is from a cave in the Sylamore Ranger District in Ozark National Forest, Arkansas (Saughey *et al.* 1978).

Order Rodentia

Family Sciuridae

Tamias striatus (eastern chipmunk)

Material.—OMNH 59511, partial skeleton recovered by screen-washing as several separated elements, but probably representing the associated parts of an individual skeleton, including: left dentary with partial i1, anterior roots of p4, and all roots of m1 (Fig. 5A); two lumbar vertebrae; partial sacrum; partial right and left ilia; complete left femur and shaft of right femur; complete left tibia; right tibia lacking proximal end; and left navicular. OMNH 70980, left dentary with p4-m2; OMNH 70983, right femur; OMNH 70982, left partial lower molar; OMNH 70981, right M1 or M2.

Discussion.—The dentary associated with OMNH 59511 lacks cheek teeth but retains a portion of the lower incisor. The diastemal region of the dentary drops only slightly anterior to the p4 (as is characteristic of the Tamiini [Black 1963], whose only known Pleistocene representatives belong to the genus *Tamias*). The enamel on the anterior face of the lower incisor is faintly ridged with five to six low ridges and shallow grooves in between. Among tamiines, the cheek teeth preserved in the second dentary (OMNH 70980) match the morphology of modern specimens of *T. striatus*. Although there is the possibility that a western or unrecognized extinct species of chipmunk could be represented by these specimens, *T. striatus* is the only chipmunk that today occurs east of the Great Plains, where it is widespread. All other known chipmunks are montane species of the western USA; none occurs any closer to Sassafras Cave today than 690 km away and on the other side of the Great Plains, which are generally unsuitable habitat for these woodland sciurids. Alveolar lengths of the cheek tooth rows (p4-m3 alveoli) for the two specimens are 6.4 and 6.8 mm. In OMNH 59511, the lower incisor measures 2.1 mm in anteroposterior diameter and 1.1 mm in transverse diameter. In

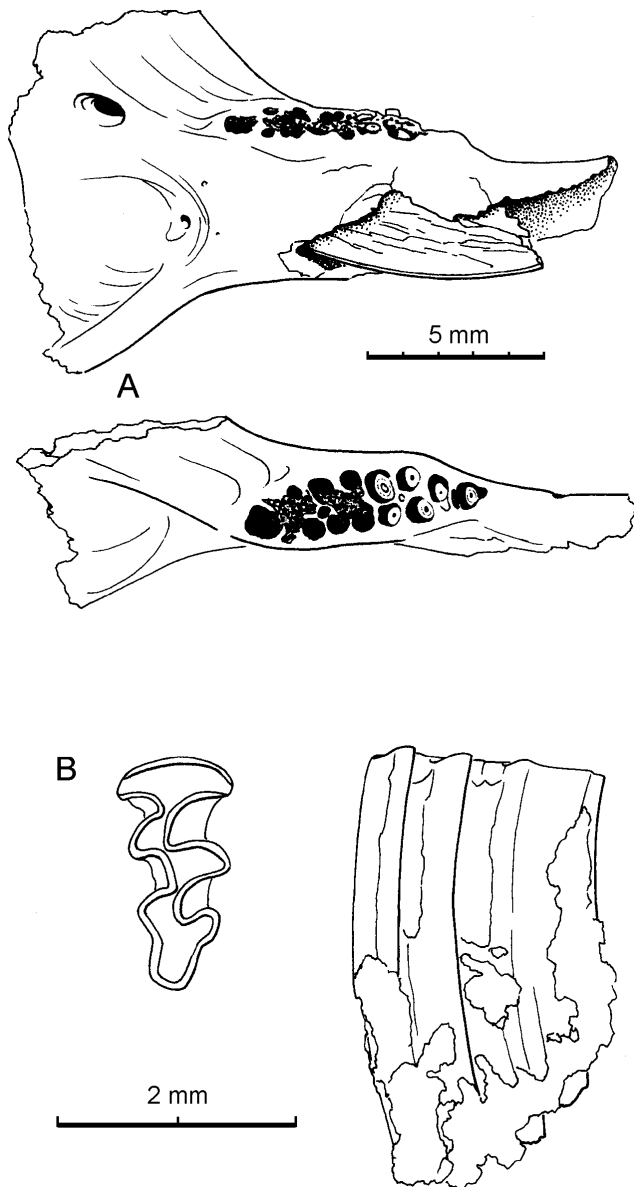


Figure 5. Rodent fossils found in Pleistocene deposit in Sassafras Cave, Oklahoma. A, *Tamias striatus*, OMNH 59511, edentulous left dentary containing broken i1 and alveoli for other teeth; shown in lingual and occlusal views. B, *Microtus* sp., OMNH 59512, right upper third molar with adhering concretion; in occlusal and labial views.

OMNH 70980, the anteroposterior length and transverse width of each of the cheek teeth (to the nearest 0.5 mm; measured according to the method of Gordon & Czaplewski 2000) are: p4, 1.35 x 1.45; m1, 1.70 x 1.75; m2, 1.95 x 1.90. The partial lower molar (OMNH 70982) is broken posteriorly but its transverse width is 1.70 mm. The upper molar is 1.60 mm in anteroposterior length and 1.95 mm in transverse width. These measurements compare very closely with those of modern *Tamias striatus pipilans* provided by Ray (1965). The Sassafras Cave specimen is much smaller than *Tamias aristus*, a large extinct chipmunk known only by a skull, jaw, and isolated cheek tooth from the Pleistocene of Georgia (Ray 1965). The chipmunk postcranial

bones from Sassafras Cave compare favorably with those of *T. striatus*, and do not pertain to *Neotoma*, *Sigmodon*, or other rodents.

In modern times, this species is common in the eastern Ozark Highland but seems to be relatively less common to the west. Its modern distribution extends westward to the eastern edge of the Great Plains, including about the eastern one-third of Oklahoma (Caire *et al.* 1989). In a late Pleistocene context, it has been reported as far west as Beaver County, Oklahoma, where it occurred in the Elm Creek local fauna (Dalquest & Baskin 1992).

Family Muridae

Subfamily Sigmodontinae

Reithrodontomys sp. indeterminate (harvest mouse)

Material.—OMNH 70979, left I1; OMNH 70978, left maxilla fragment with M1-M2.

Discussion.—The upper incisor is small, strongly grooved and broken at its base. It has the following measurements (in mm): antero-posterior diameter, 1.10; transverse width, 0.60; radius of curvature (measured according to the method of Akersten, 1981), 2.75. The maxilla fragment has moderately worn teeth that are very low-crowned. Tooth measurements are: M1 anteroposterior length, 1.40; M1 transverse width, 0.85; M2 anteroposterior length, 0.90; M2 transverse width, 0.85. The cheek teeth bear no accessory lophs or cusps. Although we refer the Pleistocene specimens from Sassafras Cave to the genus *Reithrodontomys* based on size and incisor and molar morphology, we cannot refer them to a species based on the currently available material.

Peromyscus sp. indeterminate (white-footed mouse)

Material.—OMNH 70960, right maxilla fragment with M1-M2; OMNH 70959, left m1.

Discussion.—The maxillary molars are relatively high-crowned—much more so than in the specimens referred to *Reithrodontomys*—and in a stage of light wear. There is a poorly developed mesoloph on M1 but none on M2. The M1 has a strong parastyle connected to the posterolabial portion of the anterocone. Otherwise, no accessory lophs or cusps are present. The lower first molar is lightly worn, moderately high-crowned, and lacks accessory cuspid and lophids. Measurements (in mm) of these molars are as follows: M1 anteroposterior length, 1.85; M1 transverse width, 1.15; M2 anteroposterior length, 1.45; M2 transverse width, 1.15; m1 anteroposterior length, 1.70; m1 transverse width, 0.95. As in the case of the *Reithrodontomys* specimens mentioned above, we can readily assign these specimens to the genus *Peromyscus* based on size, crown height, and molar morphology, but the sample is too small and incomplete to assign them to a species.

Subfamily Arvicolinae

Microtus sp. (vole)

Material.—OMNH 59512, right M3 (Fig. 5B).

Discussion.—The tooth measures 1.9 mm in anteroposterior length and 1.1 mm in transverse width. It has an anterior loop, two closed triangles, and a posterior loop with one weak reentrant labially and one lingually. The rootless (evergrowing) tooth overall has two labial and two lingual reentrant folds filled with cementum; no cementum occurs in the weak folds of the posterior loop.

The tooth is similar to *Microtus (Pitymys) pinetorum* and *M. (Pedomys) ochrogaster*, which tend to be distinct from most other voles in having M3 usually with only two closed triangles. Distinguishing these two species on dental characters is difficult or impossible, even when complete tooth rows are available (Guilday *et al.* 1978). Nor is it possible to differentiate among the numerous

species of *Microtus* with only an isolated M3. Both *M. pinetorum* and *M. ochrogaster* are common as Pleistocene fossils in the eastern United States.

Woodland voles (*M. pinetorum*) occur in the cave area today. As the name implies, they live in woodlands, especially in dry, mature deciduous forests where they make burrows on the forest floor in leaf litter (Semken 1984). Prairie voles (*M. ochrogaster*) are known in the general region of Sassafras Cave (in Cherokee County, immediately west of Adair County). There they select dry grasslands with enough grass to cover their runways and enough soil for their burrows; they never utilize wooded regions (Semken 1984).

Order Perissodactyla

Family Tapiridae

Tapirus veroensis (extinct tapir)

Material.—OMNH 59528, partial skeleton (Figs.6-10) including: left dentary with p2-m3; mandibular symphysis with right alveolus for i1, broken i2, root for i3, and intact c1; anterior fragment of right maxilla with C1-P2; posterior fragment of right maxilla with M1 and separate crown of M2 or M3; right and left petrosals; partial atlas; several other vertebral fragments; small fragments of ribs; partial head and distal fragment with trochlea of left humerus; distal portions of left radius and ulna; nearly complete right humerus (proximal end damaged); complete right radius and ulna; shaft of left femur missing both ends; entire left leg skeleton distal to the middle of the tibia and fibula (found in articulation; Fig.7); partial left manus including scaphoid, lunar, trapezoid, unciform, and metacarpals II, IV, and V (metacarpal IV is rodent-gnawed and chipped); partial right manus including scaphoid, cuneiform, pisiform, fragment of magnum, metacarpal III; several phalanges; sesamoids.

Discussion.—The bones are all part of one associated skeleton of a young adult. The epiphyses of all preserved bones are fully fused, and the m3 is erupting but its cross-crests are unworn. The cross-lophs of m2 are very lightly worn. Strong facets are worn into the anterior face of the c1 and the lateral side of i2 where these teeth occluded with the I3. The crown of the i2 is not *in situ* but is preserved separately. The M2 is lightly worn and M1 moderately worn.

The P1, preserved in an anterior fragment of the maxilla, is roughly triangular in occlusal outline and is not molariform. The P2 is subquadrate and fully molariform. In a separate, posterior fragment of the right maxilla, the two remaining molars can be identified as M1 and M2 based on their position relative to the anterior base of the zygomatic arch and the fact that the tooth identified as M2 has an interdental contact facet on its posterior side. The M3 was not recovered. The interdental contact facet on the anterior side of the M2 fits perfectly against the facet on the posterior of the M1 when these teeth are manually fitted together, although the M2 is not *in situ* and the remnants of its roots no longer reach their alveoli in the maxilla because of breakage and abrasion that occurred to the tooth after death and decomposition of the carcass.

Portions of the appendicular skeleton (distal parts of the arms and legs) were articulated, vertically oriented (more or less in a standing position), and well preserved where they were embedded in the cave mud. In strong contrast, the axial skeleton, girdle elements, and proximal segments of the limbs are much more poorly preserved or absent. The left rear leg was intact and articulated from the middle of the tibia and fibula distad, but the proximal halves of the tibia and fibula are absent (Figs.7 & 8). The left femur is represented by a large portion of the shaft but is missing both ends. Judging from the lighter color of the joint areas on the right forelimb (which match the preservation in the hind limb bones), it, too, was articulated or nearly so from the humerus distad. The proximal end of the right humerus is damaged

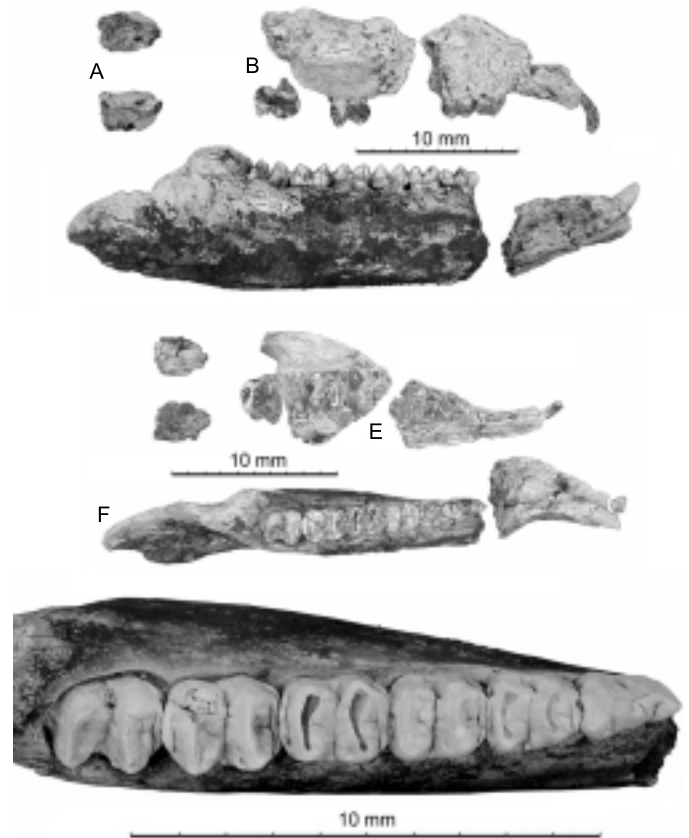


Figure 6. *Tapirus veroensis*, OMNH 59528, cranial and jaw fragments in lateral view (A-C), and occlusal view (D-G). Photos show (A, D) right and left petrosals, (B, E) right M2 or M3, and right maxilla fragments with M1 and C1-P2, (C, F) left mandibular ramus with p2-m3, and mandibular symphysis with right i2 and c1. G, close-up occlusal view of lower left cheek teeth; the teeth were coated with ammonium chloride to show surface details.

but the remainder of the bone is well preserved.

Unquestionably, this mode of preservation indicates that the animal died where its remains were found. The limbs were embedded in mud at or near the time of death and, after decomposition of the flesh the bones, remained in "life position" to the present day. It is unlikely that an animal that habitually spends much of its life wading and foraging in pools and ponds would have died from being entrapped by the sticky, fine cave mud. More likely it died of starvation, or perhaps of injuries sustained in a fall in the cave, while standing or lying in the mud or in a pool of water. The torso of its carcass and the proximal segments of its limbs were probably above the surface of this mud when it died. After the flesh decomposed, the distal limb bones embedded in the mud were preserved well, but the axial skeleton and proximal limb bones were apparently exposed to weathering within the cave. This resulted in the washing away of many axial skeletal elements and poor preservation of the few remaining pieces, which were later buried by additional mud until they were discovered and excavated.

In reviews of late Cenozoic tapirs of North America, Ray and Sanders (1984) and Jefferson (1989) each recognized a large and a small species of tapir based mainly on dental and cranial remains. In



Figure 7. *Tapirus veroensis*, OMNH 59528, lower portion of left hind leg skeleton as found articulated in the terrace deposit in Sassafras Cave. Distal halves of tibia and fibula are vertical. Knife propped against distal tibia is 18 cm long.



Figure 8. *Tapirus veroensis*, OMNH 59528, bony elements of the left hind limb. Distal limb elements are well preserved, but the femur (at right) is weathered and missing both ends.

the central and eastern United States, Ray and Sanders (1984) called the larger early Pleistocene (Irvingtonian land mammal age) species *Tapirus haysii* and the smaller late Pleistocene (late Irvingtonian and Rancholabrean land mammal ages) one *T. veroensis*. In western North America, west of the Rocky Mountains, Jefferson (1989) called the large Plio-Pleistocene species *Tapirus merriami* and the smaller one *Tapirus californicus*. *Tapirus veroensis* is indistinguishable in size from *T. californicus*, and *T. veroensis* may eventually become a junior synonym of *T. californicus* if more diagnostic specimens of *T. californicus* are found (Jefferson 1989). Several cryptic species of fossil tapirs could actually be represented by the numerous fragmentary teeth and jaws found in Pleistocene deposits in the USA if living

Table 3. Cranial measurements in mm of *Tapirus veroensis* (OMNH 59528) from Sassafras Cave, Oklahoma. Measurements follow those made by Hulbert (1995). Measurements in parentheses represent estimates of broken specimens.

Upper canine alveolar length	6.7
Upper canine alveolar width	6.5
Mandibular depth measured anterior to p2	(54.7)
Mandibular depth measured posterior to m3	72.9
Length of lower cheek tooth series (p2-m3 length)	134.7
Length of lower premolar series (p2-p4 length)	62.6
Length of lower molar series (m1-m3 length)	72.2
Lower canine alveolar length	13.7
Lower canine alveolar width	12.4
Symphysial width across the lower canines	(46.2)
Length of the mandibular symphysis	(75.0)
Diastema length between C1 and P1 alveoli	(48.4)

Central and South American *Tapirus* species are used as examples. As pointed out by Ray and Sanders (1984), the three species of tapirs living today in northern Colombia are easily differentiated in the flesh and by cranial characters, but they overlap broadly in most dental characters (Hershkovitz 1954). Numerous species names have already been applied to relatively abundant tapir fossils across the USA and Mexico, but most of the material is inadequate for specific identification. In the meanwhile, *T. veroensis* is the name that has been widely applied to small eastern U.S. tapirs.

The Sassafras Cave tapir compares favorably in the dimensions of its teeth and jaws with the small Pleistocene tapirs of the central and eastern United States (Tables 3-5). There is only one other adult tapir from the Ozark Highland that includes parts of the postcranial skeleton (Oesch 1967; Parmalee *et al.* 1967), and that specimen is larger than the Sassafras Cave specimen in most available measurements (Tables 4 & 5). Accordingly, we tentatively assign the Sassafras Cave specimen to *T. veroensis*. *Tapirus veroensis* is primarily known from sites of Rancholabrean age (Ray & Sanders 1984; Hulbert 1995); therefore, we also tentatively assign the Sassafras Cave faunal assemblage to the Rancholabrean.

DISCUSSION

The Sassafras Cave faunule is the first Pleistocene mammalian assemblage to be described from the Ozark Highland in Oklahoma. In fact, previous authors recorded only one Pleistocene vertebrate, the giant short-faced bear, *Arctodus simus*, from a cave in this part of Oklahoma (Puckette 1976; Smith & Cifelli 2000). Martin and Naples (1999) noted that there was a gap in the distribution of tapirs in eastern North America in the late Pleistocene. At that time, tapirs occurred nearly to the continental glacier front except for an area more-or-less centered along what is now the Oklahoma-Arkansas political boundary. They suggested that Pleistocene tapirs in North America were more limited by the density of aquatic-margin vegetation than by temperature. In any case, this record from Sassafras Cave, Oklahoma, and that of Martin and Naples (1999) from Kansas now fill the former gap in the



Figure 9. *Tapirus veroensis*, OMNH 59528, bony elements of the forelimbs including complete right humerus, radius, and ulna, distal left radius and ulna, and several carpals, metacarpals, and manual phalanges.

Pleistocene distribution of tapirs.

Outside of caves, there were three previous localities in which Pleistocene tapirs occurred in Oklahoma. Two of these localities yielded early Pleistocene (Irvingtonian) specimens and one is of unknown age. One Irvingtonian record is at Bowles gravel pit near Chickasha, Grady County, where a palate with all the cheek teeth (OMNH 9568) and an isolated left metatarsal III (OMNH 16504) were found (Stovall & Johnston 1934; Strain 1937). The other Irvingtonian record of

Table 4. Tooth measurements in mm of *Tapirus veroensis* (OMNH 59528) from Sassafras Cave, Oklahoma, and of another adult specimen (CM 159; Central Missouri State College, Warrensburg, Missouri) from Crankshaft Cave, Missouri, as provided by Oesch (1967) and Parmalee *et al.* (1967).

Tooth	length		anterior width		posterior width	
	OMNH 59528	CM 159	OMNH 59528	CM 159	OMNH 59528	CM 159
P1	18.3	21.2	12.0	12.5	15.7	18.8
P2	19.0	20.0	21.2	23.4	23.1	15.0
M1	23.2	22.7	26.6	27.3	23.8	25.0
M2	26.0	25.3	28.6	30.9	24.9	27.0
p2	21.4	24.7	11.2	—	14.3	16.5
p3	20.3	22.3	15.6	16.8	17.1	19.3
p4	21.1	21.3	18.4	20.4	18.5	21.3
m1	23.0	28.7	18.9	19.9	17.6	19.2
m2	25.2	26.3	19.8	21.8	18.9	21.3
m3	24.8	—	19.2	—	17.1	—

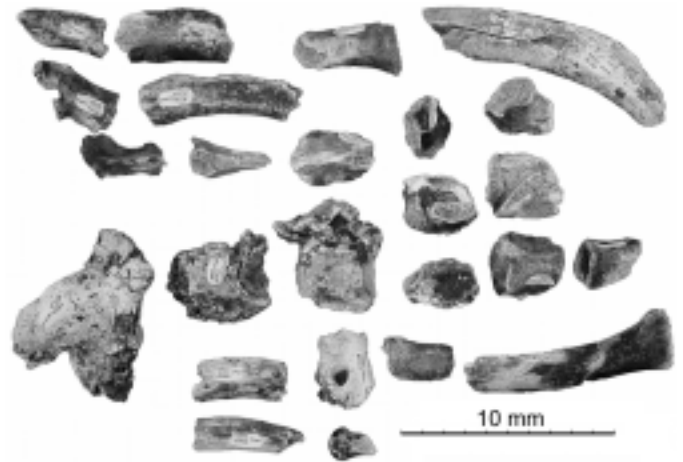


Figure 10. *Tapirus veroensis*, OMNH 59528, selected elements from the axial skeleton showing poor preservation. Atlas fragment at lower left.

T. haysii is from the Holloman gravel pit near Frederick, Tillman County, where a right dentary containing dp3, dp4, p3, p4, and m1 was found (Midwestern State University specimen no. 9238, now housed at the Texas Memorial Museum; Hay & Cook 1930; Dalquest 1977; Ray & Sanders 1984). All three of these specimens represent *Tapirus haysii* and are larger than the Sassafras Cave tapir. The third locality was reported by Troxell (1917), who merely included “tapir” among a list of other fossil vertebrates from a channel-fill deposit near Mulhall, Logan County, but gave no other information. The whereabouts of the Mulhall specimen, the skeletal element and species represented, and age of this specimen are unknown.

Beyond Oklahoma, other Ozark Highland records of Pleistocene tapirs include Peccary Cave and Ten Mile Rock in Arkansas, and Crankshaft Cave, Boney Spring, Jones Spring, and Enon Sink in Missouri (Mehl 1962; Oesch 1967; Parmalee *et al.* 1967; Saunders 1977; Faunmap Working Group 1994), but records of the genus *Tapirus* are widespread elsewhere in Pleistocene localities across the southern half of the United States (except in mountainous regions of the West) and Mexico (Kurtén & Anderson 1980; Jefferson 1989; Faunmap Working Group 1994; Arroyo-Cabrales *et al.* 1996).

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Table 5. Measurements of postcranial bones (in mm) of *Tapirus veroensis* (OMNH 59528) from Sassafras Cave, Oklahoma. Measurements follow those made by Hulbert (1995), where preserved in the Oklahoma specimen. Abbreviations: trw = transverse width; apl = anteroposterior length. Measurements of another adult specimen (CM 159; Central Missouri State College, Warrensburg, Missouri) from Crankshaft Cave, Missouri, as given by Oesch (1967) and repeated by Parmalee *et al.* (1967), are provided in brackets for comparison, where available.

	Humerus	Radius	Femur	Tibia	
Greatest length		222.2			
Midshaft transverse width	31.5 [34.0]	29.6	39.0	30.2	
Midshaft anteroposterior length	37.4	21.0	35.3 [34]	32.5	
Proximal articular width		54.1			
Proximal articular apl		30.1			
Greatest distal width	70.8	60.8		52.7	
Width of distal articular surface	54.9				
Distal apl		37.9		43.5	
	Metacarpal	II	III	IV	V
Greatest length	99.3 [111.7]	120.8 [135.2]	97.1 [106.9]	74.2 [83.4]	
Midshaft trw	20.3	28.6	19.8	12.2	
Midshaft apl	12.0	13.4	12.3	10.8	
Proximal articular width	22.9	31.7	21.3	15.1	
Proximal articular apl	20.5	24.0	23.0	20.8	
Distal articular width	20.7	29.1	21.0	17.7	
Distal articular apl	23.1	22.8	21.9	19.2	
	Astragalus	Calcaneus			
Greatest length		106.6 [110]			
Medial length	53.3				
Lateral length	61.6 [64]				
Medial length of trochlea	43.7				
Greatest transverse width	56.4 [53]	49.3			
Greatest apl		49.1			
Distal articular width	49.2				
Distal articular apl	27.2				
	Metatarsal	II	III	IV	
Greatest length	102.3 [114]	120.1 [133]	103.6 [114]		
Midshaft trw	19.6	26.3	18.7		
Midshaft apl	13.8	16.3	14.0		
Proximal articular width	18.5	31.9	23.4		
Proximal articular apl	25.9	33.9	25.4		
Distal articular width	21.4	30.2	21.4		
Distal apl	25.6	25.2	25.5		

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