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TERTIARY BATS (MAMMALIA: CHIROPTERA) FROM NORTHERN NEBRASKA

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ABSTRACT

Scarce remains of bats are reported from five localities in northern Nebraska in which other kinds of vertebrates are much more common. *?Oligomyotis* or *?Myotis*, possibly of an undescribed species, is represented by fragments of jaws and humeri from an early Arikareean (late Oligocene) locality in Dawes County. Several toothless jaw fragments from the late Hemingfordian (middle Miocene) Companion Quarry in Sioux County represent an indeterminate microchiropteran. An indeterminate species of *Myotis* was encountered in the middle Clarendonian (late Miocene) Ashfall site in Antelope County. A hairy-tailed bat, *Lasiurus* sp. indet., occurred in late Clarendonian (late Miocene) and late Blancan (late Pliocene) sites in Brown and Antelope counties, respectively. The Clarendonian record for *Lasiurus* represents the earliest documented occurrence of the genus.

† † †

In general, fossils of bats are rare in North America. Because of their small size, the fragility of their bones, and their secretive habits, bats have a limited chance of becoming fossilized except in caves. Fluvio-lacustrine sedimentary deposits usually reflect open areas where bats and their bony remains are unlikely to be preserved, especially in comparison to caves or karstic areas (Sigé and Legendre 1983, Kowalski 1995). The paleo-cave or paleo-karstic record of bats, too, is biased toward cave-inhabiting species, which tend to concentrate in large colonies. In contrast, open areas are often inhabited by tree-roosting bats, which tend to be solitary or roost in small numbers and are widely dispersed.

Fluvio-lacustrine sedimentary rocks of Tertiary age in Nebraska have produced scarce, fragmentary remains of Microchiroptera from scattered localities and a broad span of time. The specimens range in age from late Eocene to Pliocene. In northwestern Nebraska, Ostrander (1983, 1985) reported the vespertilionoids

Chadronycteris rabenae Ostrander, 1983, and *Stehlinia?* sp. (both assigned by Ostrander to the Kerivoulidae), from the Raben Ranch and Dirty Creek Ridge local faunas of the Chadronian land mammal age (LMA) in Sioux County (Fig. 1A). These are the only Paleogene faunas in Nebraska that include bats. At the time Ostrander reported these finds, the Chadronian LMA was considered to represent the early Oligocene, however, it is now considered to fall almost entirely within the late Eocene (Prothero 1995). The two Chadronian local faunas have a Paleogene character in that they suggest a tropical or subtropical forest habitat with frost-free climate. The Raben Ranch local fauna includes fish, amphibians, reptiles, and such mammals as marsupials, primates, diverse insectivorans and rodents, carnivorans, brontotheres, rhinocerotids, and artiodactyls, as well as the largest known single accumulation of Oligocene multituberculates (Ostrander 1983).

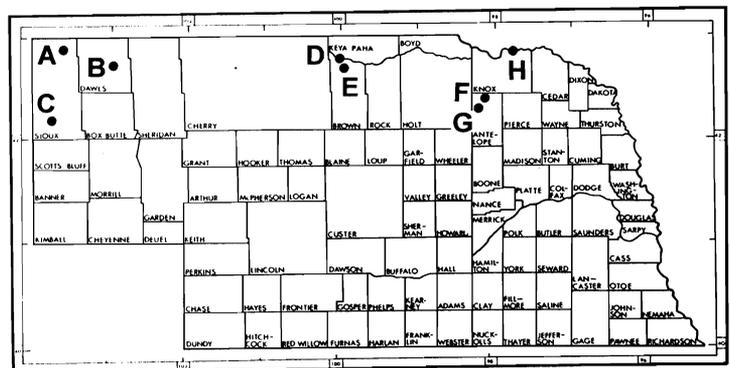


Figure 1. Map of Nebraska showing localities at which Tertiary bat fossils have been discovered in northern Nebraska. A, Raben Ranch; B, Dw121; C, Companion Quarry (Sx128); D, Norden Bridge Quarry (Bw106); E, Pratt Slide (Bw123); F, Ashfall (Poison Ivy; Ap116); G, Big Springs (Ap103); H, Annie's Geese Cross (Kx110).

In the northeastern part of Nebraska, sediments of the Valentine Formation interred bats at two localities. At the Norden Bridge Quarry, Brown County, Voorhies (1990) reported cf. *Antrozous* sp. in a middle Barstovian LMA fauna (ca 14.5–13 Ma; Fig. 1D). Czaplewski (1991) reported the vespertilionids *Potamonycteris biperforatus* and cf. *Myotis* from a locality known as Annie's Geese Cross, Knox County, which includes a late Barstovian LMA fauna (ca 13–12 Ma; Fig. 1H). The Norden Bridge local fauna is extensive and suggestive of a frost-free climate and open grassy or savanna habitat with extensive (floodplain?) forests (Voorhies 1990). Obligate forest dwellers include flying squirrels, and possible forest dwellers include brachydont subungulates and ungulates, among which browsers are twice as common as grazing forms.

In southern Nebraska, the Valentine Formation produced one of the largest accumulations of Tertiary Chiroptera in North America. These specimens, originally reported by Corner (1976), have not yet been studied in detail, but at least two species of Vespertilionidae are represented by abundant skeletal remains in the Myers Farm fauna, Webster County, of late Barstovian LMA (13–12 Ma).

In this paper we document several additional occurrences of bats in the Tertiary fossil record of Nebraska. The new specimens range in age from the late Oligocene to the late Pliocene. They come from four different localities, discussed below from oldest to youngest. Although the specimens are fragmentary and identifiable to the generic level at best, they constitute important records in light of the generally poor fossil record of bats in the Tertiary of North America.

Dental terminology follows Menu (1985) and terminology for the morphological features of the humerus follows Vaughan (1959). Specimens were identified by comparison with skeletal material of modern bats and, where available, casts or originals of fossil specimens. These same references plus the illustrations and descriptions in Felten et al. (1973), Galbreath (1962), Lawrence (1943), Smith (1972), and Yoon and Uchida (1983) were used as a partial basis for identification of humeri.

LOCALITIES AND DESCRIPTIONS OF SPECIMENS

Dw121, Dawes County—?*Oligomyotis* or ?*Myotis* sp. indet.

This locality (UNSM Dw121; Fig. 1B) is south of Chadron, Nebraska, and is where specimens were recovered from a sand and gravel channel near the base of the Arikaree Group. The channel lies along the axis of the northern Gering paleovalley of Swinehart et al.

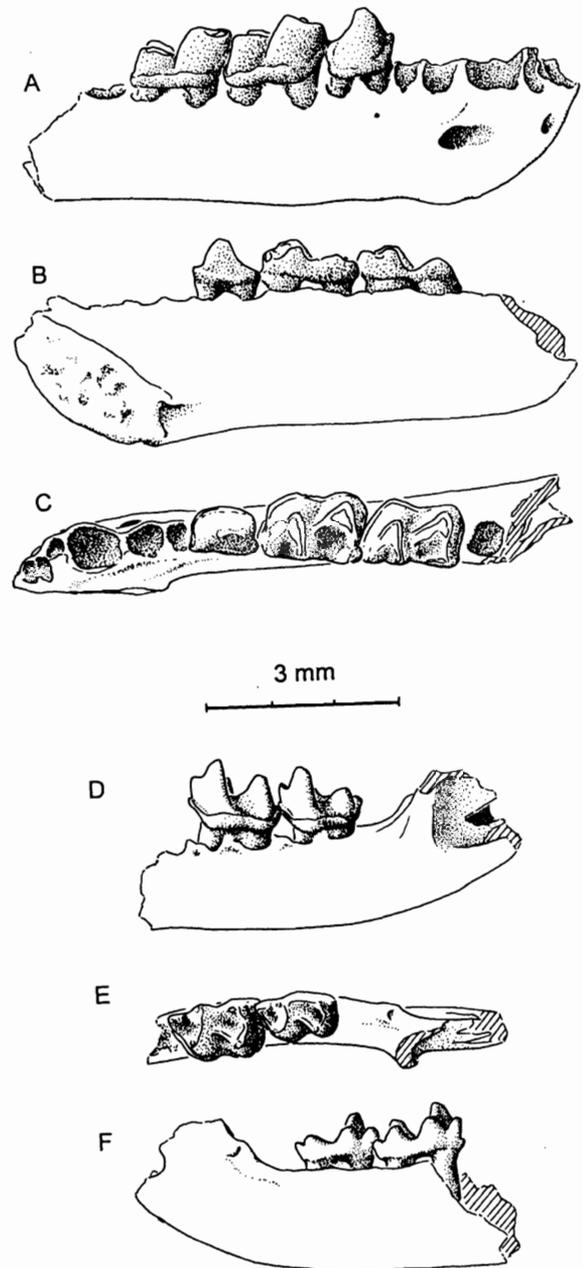


Figure 2. ?*Oligomyotis* or ?*Myotis* from UNSM locality Dw121. Right dentary fragment with p4–m2 (UNSM 26538) in A, labial, B, lingual, and C, occlusal views. Left dentary fragment with m2–m3 (UNSM 26539) in D, labial, E, occlusal, and F, lingual views. Hatching indicates broken area.

Table 1. Measurements (in mm) of early Arikareean teeth and jaws of ?*Myotis* or ?*Oligomyotis* from UNSM locality Dw-121, Dawes County, Nebraska.

UNSM no.	dentary depth*	p4		m1			m2			m3		
		apl	tw	apl	trigw	talw	apl	trigw	talw	apl	trigw	talw
26536	—						1.6	1.05	1.1	1.4	0.9	0.7
26538	1.6	1.1	0.8	1.7	1.2	1.3	1.7	1.1	1.05			
26537	1.8			1.6	1.05	1.2	1.4	1.0	0.9			
26539	1.3						1.4	0.9	0.95	1.3	0.8	0.7
26543	1.75	1.0	0.8	1.6	1.0	1.2	—	1.1	—			

*Measured on the labial side from the bottom edge of the alveolus of the anterior root of the m2 to the inferior edge of the dentary.

(1985). The fauna is assigned to the early Arikareean LMA (late Oligocene) based on a preliminary analysis of mammalian taxa which include the erinaceoid insectivore *Ocajila* and the rodent *Geringia* (Bailey 1992, Tedford et al. 1996).

Eleven bat specimens were discovered at this locality, including fragments of jaws and humeri, an isolated lower molar, and an isolated upper canine. The jaw fragments include UNSM 26536–26539 and 26543. The horizontal ramus of one dentary (UNSM 26538; Fig. 2) is nearly intact except for the posterior end; length of the alveolar tooth-row from c1-m3 can be estimated to have been 7.7 mm. Based on morphology of the teeth, the jaws appear very similar or identical to those of *Myotis*. Based on measurements of the teeth and jaws, two different sizes appear to be present (Table 1). Measurements of UNSM 26536 and 26538 are approximately equivalent to one another in size, as are measurements of UNSM 26537 and 26539 (Fig. 2); the first pair of specimens are larger than the last pair. The difference is especially apparent in the size of the m2. In the first pair, m2 length is 1.6–1.7 mm; in the last pair, both specimens measure 1.4 mm. Thus, the first pair are roughly 15% larger in m2 length than the last pair. There also seems to be a difference in the proportions of the p4, as seen in occlusal view, between the two available specimens preserving this tooth. In UNSM 26538 the occlusal outline of p4 appears to be slightly longer relative to its width than in UNSM 26543. The size difference is unlikely to be attributable to sexual dimorphism. For example, only minor sexual dimorphism in jaw size (0.2–1.1% in condylocanine length) occurs in North American *Myotis* species, and the differences are not statistically significant (Williams and Findley 1979). The difference among the Dw121 specimens seems to be beyond that expected within one species. It is more likely that two different species are represented, and these possibly pertain to the genus *Myotis*. Nevertheless, a better sample is necessary to say definitively whether more than one species is present

at this locality.

In addition to the jaw fragments, the proximal portion of a humerus (UNSM 26540) and the distal portions of two humeri (UNSM 26541 and 26547; Fig. 3) were recovered at this locality. Measurements of UNSM 26540 are: greatest proximal width, 3.2 mm; diameter of head, 1.9 mm; extension of greater trochanter beyond level of head, 0.2 mm. Greatest width of the distal epiphyses of UNSM 26541 and 26547 is 3.0 mm. The two distal fragments appear to belong to the same species. The spinous process is broken off each of these fragments, and both are abraded and damaged about the edges, so that some distinguishing features are missing.

In each of the distal fragments of humeri, the epitrochlea is relatively wide. Only a tiny bit of the shaft is preserved in either specimen. When viewed from the anterior, the distal epiphysis appears not to be displaced laterally (as in many bats); a vertical line drawn along the medial edge of the trochlea would probably have passed well to the outside of the plane of the medial edge of the shaft. The preserved portion of the spinous process sweeps slightly posteriorly and is separated from the epitrochlea by a distinct groove. The olecranon fossa occurs as a moderate depression with a relatively distinct proximal border.

An interesting difference between the two humerus fragments occurs in the lateral epicondyle. In UNSM 26541 the tiny notch for origin of the extensor carpi radialis longus and brevis is exceedingly shallow by comparison with modern vespertilionids, and the adjacent, tiny, proximally-directed projection on the lateral ridge of the capitulum of most vespertilionids is not developed. In lateral view, the notch passes more than half way across the shaft of the bone. This condition is like that described by Galbreath (1962) for the lateral epicondyle in the humerus of *Oligomyotis casementi*. In the other specimen, UNSM 26547, the notch is deeper than in UNSM 26541 but still relatively shallow, and the

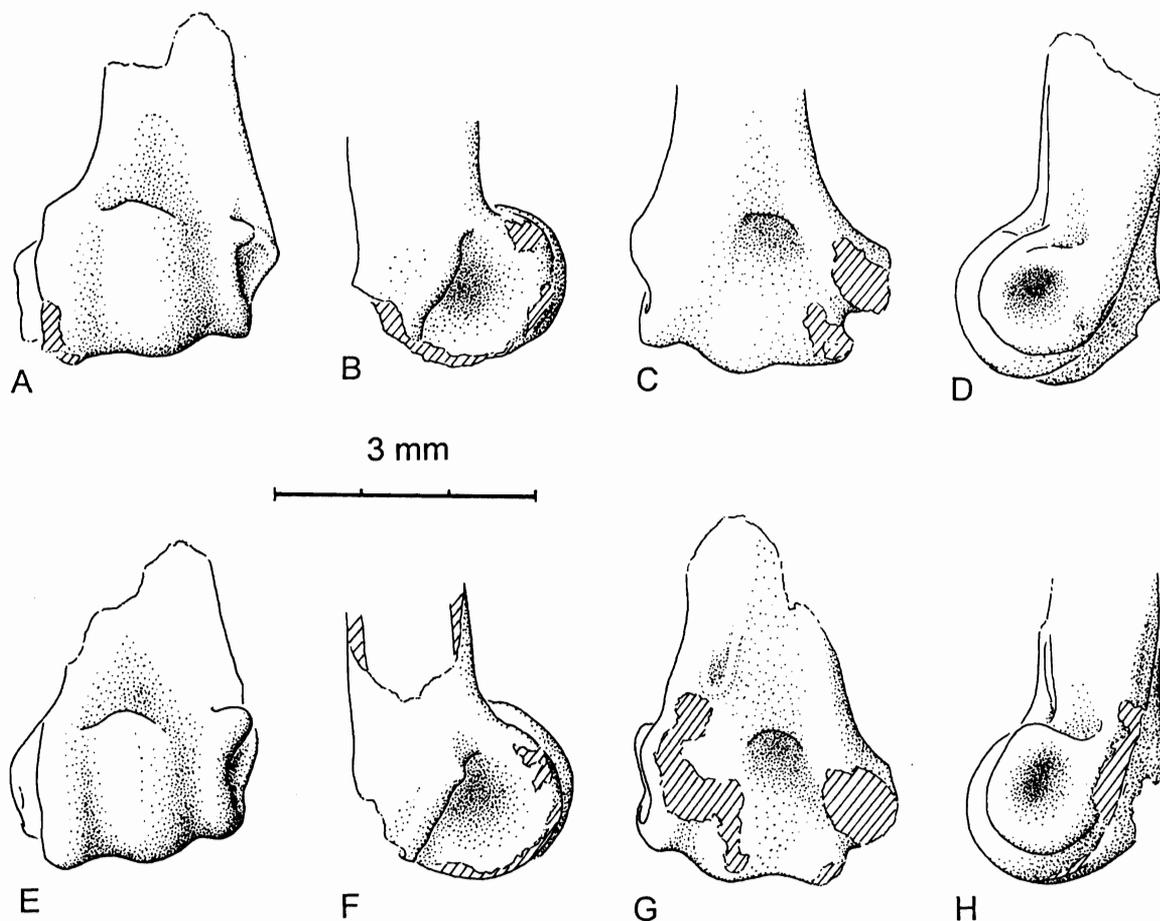


Figure 3. ?*Oligomyotis* or ?*Myotis* from UNSM locality Dw121. Distal fragment of the left humerus (UNSM 26541) in A, anterior, B, medial, C, posterior, and D, lateral views. Distal fragment of left humerus (UNSM 26547) E, anterior, F, medial, G, posterior, and H, lateral views. Hatching indicates breakage.

tiny projection on the lateral ridge of the capitulum is present but very short and blunt, unlike most other vespertilionids.

Although these humeral fragments are not well preserved, they are consistent in some details of shape with the humerus of *Oligomyotis casementi*, a monotypic species known only from a distal humerus fragment from the Orellan (middle Oligocene) of Colorado (Galbreath 1962). An attempt to locate and borrow the holotype humerus (the only known specimen) of *Oligomyotis casementi* was unsuccessful, but the following remarks are based on comparisons with the figure and description provided by Galbreath (1962). Similarities of the specimens from Dw121 to the humerus of *Oligomyotis* include (1) the occurrence of the groove between spinous process and trochlea, (2) the rounded rather than keeled nature of the medial ridge of the capitulum, (3) the shallowness of the notch proximal

to the lateral epicondyle, and (4) the absence of the projection on the lateral ridge of the capitulum. (The last of these similarities pertains only to one of the two Nebraskan specimens.) The Nebraskan humeri differ from *Oligomyotis casementi* most notably (1) in being much smaller and (2) in having the vertical edge of the trochlea apparently well outside rather than inside the plane of the medial edge of the shaft. In addition, unlike *Oligomyotis*, the Nebraskan humeri (3) lack the large, deep, rounded, medially-facing fossa on the side of the epitrochlea (for the origin of the Mm. pronator teres or palmaris longus), (4) flare at the margin of the lateral ridge of the capitulum, and (5) lack a transversely-divided radial fossa.

The humerus is known in only two other kinds of extinct vespertilionids in North America (*Miomotis floridanus* and *Suaptenos whitei*), both of which are reported only from the Hemingfordian LMA (early Mi-

ocene) Thomas Farm locality, Florida (Lawrence 1943). The genus *Miomotis* is possibly related to *Myotis*; *Suaptenos* is similar to *Eptesicus* (Lawrence 1943, G. S. Morgan pers. comm.). The Dawes County humeri differ from *Suaptenos* in their smaller overall size, in having a distinct olecranon fossa, in having the distal epiphysis less displaced laterally from the shaft, and in having the small notch immediately proximal to the lateral ridge of the capitulum longer. The specimens from Dw121 are near in size to humeri of *Miomotis*, but differ in having a distinct olecranon fossa and in having a spinous process inclined backward rather than being more-or-less parallel with the shaft.

The Nebraskan fragments agree in some morphological details with humeri of *Myotis*. However, they differ from *Myotis* in lacking the deep, tiny notch immediately proximal to the lateral ridge of the capitulum and in lacking the small, proximally-directed protuberance on the lateral ridge of the capitulum. They differ even further from the humeri of other extant genera of Vespertilionidae such as *Eptesicus*, *Corynorhinus*, *Nycticeius*, *Lasionycteris*, *Pipistrellus*, and *Antrozous*.

In summary, the humeri fragments from Dawes County, Nebraska, share some features and lack other features that are thought to be diagnostic of *Oligomyotis casementi*. They also share some features and lack others seen in humeri of *Myotis*. The jaw fragments appear to be very similar or identical to *Myotis*. The teeth of *Oligomyotis* are unknown. The Dw121 specimens were recovered by screenwashing, so the jaws and humeri may not be associated or represent the same species. It is impossible to determine the species to which the Dawes County specimens pertain, but the humeri, at least, may represent an unnamed new species of *Oligomyotis* or a related, unnamed genus. Because more than one species of bat is present in the locality (judging from the different sizes of teeth), it seems less likely but possible that all the specimens partly or entirely represent extinct species of *Myotis*.

As noted above, *Oligomyotis casementi* is known only by a single specimen from Orellan LMA deposits in northeastern Colorado. Some 22 extinct and 84 extant species of *Myotis* are known around the world. Only one Tertiary record of *Myotis* from North America is identified beyond the generic level, *Myotis* cf. *yumanensis* from the Clarendonian LMA of Oklahoma (Dalquest et al. 1996). The genus is less common as a fossil in North America than in Europe. In the Recent fauna, *Myotis* is among the most cosmopolitan genera of mammals, and is one of the most speciose genera of bats; at least five species occur in the Recent fauna of Nebraska (Czaplewski et al. 1979).

Companion Quarry, Sioux County—*Microchiroptera* indet.

This locality (UNSM Sx128; Fig. 1C) occurs in southern Sioux County in an outlier of the Sheep Creek Formation probably near the base of the Formation. Screenwashing of sediments yielded a concentration of small vertebrates including a moderately diverse fauna of late Hemingfordian LMA (middle Miocene, 16–17 Ma; Bailey and Mead 1998). The fauna was recovered from fluvial deposits and is interpreted as a predominantly autochthonous, riparian community. It is surprisingly similar to the temporally equivalent Split Rock local fauna that originated from eolian sediments in central Wyoming (Munthe 1988). The Companion Quarry fauna includes the horse *Merychippus primus* and artiodactyl *Cosoryx wilsoni* as well as an unidentified lagomorph, heteromyid, mylagaulid, and zapodid rodents, and five genera of insectivorans (Bailey and Mead 1998).

Ten specimens of bats are known from this locality. One is an isolated canine (UNSM 26575) and nine are edentulous dentaries or dentary fragments (UNSM 26573, 26574, 26576–26582). The canine is a broken upper right tooth that is missing the apical half of the main cusp. The tooth is robust, with a strong root that is nearly aligned with the axis of the crown. There is a basal cingulum that encircles all but about one-sixth of the tooth on the anterolabial side. A tiny interdental contact facet is worn onto the posterolabial portion of the cingulum, indicating the presence of an adjacent premolar. The main cusp of the canine is relatively complex in that it possesses several longitudinal ridges and grooves. The anterolabial face is convex with an indistinct, low, rounded ridge descending the main cusp at least to the level at which the tooth is broken. The posterolingual and posterolabial faces are broadly concave. Between these concave faces is a sharp posterior crest. There is also a sharp crest descending the medial side of the main cusp. Ahead of the medial crest is a well-developed groove on the anteromedial face of the crown.

Similar complex canines are found in insectivorous members of several families of bats (Freeman 1992). In general, the upper canine from Companion Quarry resembles that of vespertilionid bats but cannot be ascribed to a particular genus. The multiple crests of the tooth do not resemble the simpler crowns of upper canines of *Myotis* or genera belonging to extinct Paleogene families (upper canine “Type A” of Menu 1985). Nor is the Companion Quarry canine as laterally compressed and hemiconical as those of Menu’s upper canine “Type C” (as in *Eptesicus* and *Histiotus*, for example). It also lacks the complete cingulum of *Eptesicus* and *Histiotus*.

Despite the relative abundance of the lower jaw fragments, their lack of teeth and the fact that all are water-worn makes it difficult to identify the specimens. All appear to belong to the same species. In each, the dentary is relatively robust. The mandibular symphysis is short and deep and inclined forward; it has a teardrop-shaped outline. Three two-rooted molars were present, as in virtually all New World bats. Based on two of the better-preserved specimens, there were three lower incisors with staggered roots. Posterior to the canine alveolus are three alveoli for premolars. In two specimens, broken and water-worn roots are present in the premolar alveoli. In one jaw fragment a heavily water-worn, two-rooted posterior lower premolar still occupies the two posterior premolar alveoli. The crown of this premolar is gone but the specimen clearly indicates the presence of a small, single-rooted anterior lower premolar and a larger, two-rooted posterior premolar in this species. Thus, the lower dental formula of the Companion Quarry bat is $i3, c1, p2, m3$. A large lateral mental foramen is present usually between the roots of the canine and anterior premolar (in 6 specimens), but in one specimen is slightly farther back (beneath the anterior premolar alveolus, entering between it and the anterior root of the posterior lower premolar). The fossa for insertion of the zygomaticomandibularis muscle, partly preserved in several specimens, is deep. An insertion scar for the temporalis muscle is preserved in a few of the specimens as an angled, flat area on the medial side of the anterior base of the coronoid process.

The Companion Quarry dentary fragments indicate a bat about the size of the modern species *Lasiurus cinereus* (but with a different alveolar formula). The dentaries are much shorter and shallower than in Recent *Eptesicus fuscus*. The distance between the posteriormost molar alveolus and the ascending leading edge of the coronoid process is less than in *Eptesicus fuscus* (in which there is a small gap) and about the same as in *Lasiurus cinereus*. It is not possible to identify these specimens, but they may belong to the Vespertilionidae.

Ashfall site, Antelope County—*Myotis* sp. indet.

This locality (UNSM Ap116; Fig. 1F) was formerly known as the Poison Ivy Quarry. It is now better known as the Ashfall Fossil Beds State Historical Park, at which a herd of rhinoceroses (*Teleoceras major*) and other vertebrates were killed and buried by a volcanic ash fall (Voorhies and Thomasson 1979). The level from which the bat fossil was recovered is in the Cap Rock Member of the Ash Hollow Formation and bears a fauna of middle Clarendonian LMA (late Miocene), ca 10 Ma. Voorhies and Thomasson (1979) noted that the plant and vertebrate fossil evidence suggested a mesic,

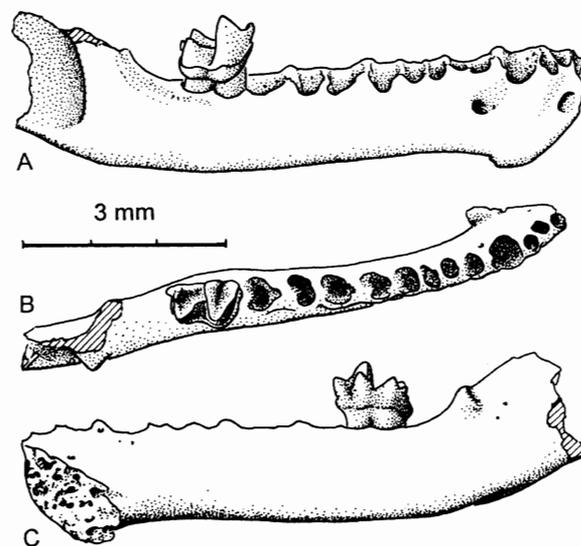


Figure 4. *Myotis* sp. indet. from UNSM locality Ap116. Horizontal ramus of right dentary with m3 (UNSM 27898) in A, labial, B, occlusal, and C, lingual views.

lacustrine paleoenvironment at this site. They envisioned nearby a broad, flat savanna periodically inundated by flood waters. Fossils of the extinct needlegrass *Berrichloa communis* are abundant in the Poison Ivy Quarry; another needlegrass (*B. primaeva*), other grasses, sedges, and rushes, and the hackberry tree *Celtis occidentalis* occur less commonly (Thomasson 1987).

The sole specimen (Fig. 4) of a bat from this locality is a right dentary preserving the m3 and the empty alveoli for all the other teeth (UNSM 27898). It was discovered in a silty sand in grid square XI between 10 and 50 cm below the base of the volcanic ash that contains articulated skeletons of rhinoceroses. The dentary is complete except for parts of the ascending ramus, from which the coronoid, condyloid, and angular processes are missing. There are alveoli for three incisors, canine, two single-rooted and one double-rooted premolars, and three molars. Mental foramina are positioned beneath the first incisive alveolus (i1) and below the alveolus for the anteriormost premolar (p2). The depth of the dentary bone measured on the labial side at the anterior alveolus of m1 is 1.01 mm; the depth at the anterior alveolus of m3 is 1.21 mm. The m3 has a strong labial cingulum and a well-developed (unreduced, with a large hypoconulid) talonid that exhibits myotodonty. The molar measures 1.29 mm in anteroposterior length, 0.90 mm in transverse width of the trigonid, and 0.71 mm in transverse width of the talonid. The alveolar formula, shape of the dentary bone, positions of the mental foramina, and shape of

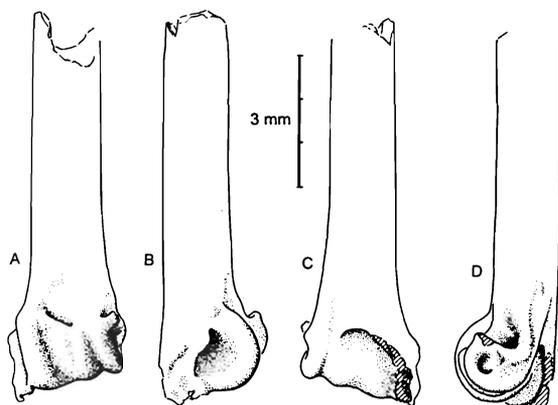


Figure 5. *Lasiurus* sp. indet. from UNSM locality Bw123. Distal end of left humerus (UNSM 100140) in A, anterior, B, medial, C, posterior, and D, lateral views.

the m3 correspond with those of *Myotis*. Unfortunately, without more complete specimens it is not possible to assign the Ashfall specimen to a species.

Pratt Slide, Brown County—*Lasiurus* sp. indet.

This locality (UNSM Bw123; Fig. 1E), also known as Pratt Quarry, occurs in the Merritt Dam Member of the Ash Hollow Formation. It was described in more detail by Skinner and Johnson (1984). The bat fossil discussed below was collected from the base of the fluvial channel described by Skinner and Johnson (1984). The locality has produced a diverse vertebrate fauna of the late Clarendonian LMA (late Miocene; ca 9 Ma). The fauna includes mixed grassland and woodland forms; a frost-free climate and permanent streams are indicated by the presence of *Alligator mefferdi* and *Tapirus johnsoni*.

A single bone belonging to a bat has been found in the rich microvertebrate fauna at this locality. It consists of the distal portion of a left humerus (UNSM 100140; Fig. 5). As is typical of Vespertilionidae, the distal articular head is not displaced dorsally but is directly in line with the shaft. The shaft of the humerus is broad in comparison with the distal epiphysis. The tip of the spinous process is missing because of breakage, but the process extends distal to the level of the distal end of the trochlea and is attached to the trochlea. The olecranon fossa is deep, especially medially, where it forms a groove lateral to, and is partly overhung by, the posterolateral edges (broken) of the medial epicondyle and its spinous process. The olecranon fossa extends behind the trochlea but not behind the inner ridge of

the capitulum. The radial fossa is shallow. A deep central cavity penetrates the medial side of the trochlea anterior to the medial epicondyle; a portion of this cavity extends distally toward the spinous process. Measurements of the specimen are: anteroposterior diameter of humeral shaft at its broken end, 1.50 mm; transverse diameter of shaft at its broken end, 1.61 mm; transverse width of distal epiphysis of humerus, 2.82 mm. Thus, the humerus fragment is approximately comparable in size to that of the extant species *Lasiurus ega* or to a fossil humerus referred to *Lasiurus fossilis* by Thewissen and Smith (1987).

The olecranon fossa is either lacking or is shallow in most New World genera of Vespertilionidae. A groovelike olecranon fossa is characteristic of *Lasiurus*. According to Lawrence (1943), a groovelike fossa is also seen in Old World *Nyctalus*, but unlike that of *Lasiurus*, it extends behind the capitulum. A deep olecranon fossa is seen in *Pipistrellus pipistrellus*, but that species has an enlarged, tubercle-like lateral epicondylar crest, absent in the Pratt Slide fossil. As in *Lasiurus*, the olecranon fossa of *Miniopterus* is deep and does not extend behind the capitulum, but the humerus of *Miniopterus* has a greatly elongated spinous process and its capitulum is divided between the inner and lateral capitular ridges by a very deep groove. *Vespertilio* has an olecranon fossa rather similar to that of *Lasiurus*, but it differs in that there is only a shallow pit anterior to the medial epicondyle and base of the spinous process.

Thus, the fragment clearly can be referred to the genus *Lasiurus* based on the features preserved. It compares well in shape to a humerus referred to *Lasiurus fossilis* by Thewissen and Smith (1987) (although postcranial elements of *L. fossilis* have not yet been found in direct association with known cranial material of that species). *Lasiurus fossilis* is known only from the type specimen, a dentary with p4-m2, and one other jaw fragment with m1-m2 from the late Pliocene (early Blancan LMA) Rexroad fauna, Kansas. The humerus from Idaho described by Thewissen and Smith (1987) was assigned to *L. fossilis* because of its similar age and overall similarity to the humeri of modern *Lasiurus* species. My measurements of the Idaho specimen are: anteroposterior diameter of shaft at a level equivalent to that at which UNSM 100140 is broken, 1.50 mm; transverse diameter of shaft at the same level, 1.69 mm; transverse width of distal epiphysis, 3.19 mm.

The humerus from Pratt Slide has a stout shaft similar to that of the Idaho specimen but it has a smaller distal head (in proximodistal diameter of the trochlea, as seen in medial view). Because of the lack of more complete skeletal material, it is not possible to

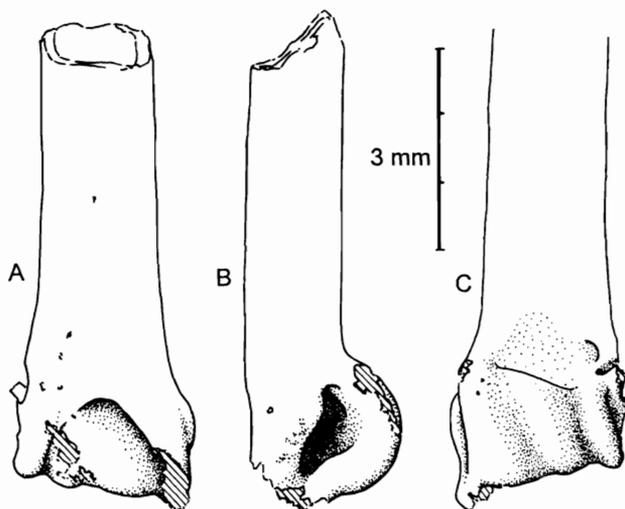


Figure 6. *Lasiurus* sp. indet. from UNSM locality Ap103. Distal end of left humerus (UNSM 75994) in A, posterior, B, medial, and C, anterior views.

assign the Pratt Slide specimen to a species.

Big Springs, Antelope County—*Lasiurus* sp. indet.

This locality (UNSM Ap103; Fig. 1G) is in the Long Pine Formation and includes a vertebrate fauna indicative of the late Blancan LMA (Rogers 1984), late Pliocene (ca 2–2.5 Ma; Lundelius et al. 1987). Based on the herpetofauna (Rogers 1984), the paleoenvironment included a temperate climate with mild winters and mild summers, where grew tall grass prairie with some intermingled strips of deciduous woods, and a permanent river nearby. Three bat specimens have been recovered at this site. They include a fragment of a humerus, an edentulous dentary, and a dentary fragment with m3. All three elements appear to be referable to the hairy-tailed bats, genus *Lasiurus*.

The distal fragment of a left humerus (UNSM 75994; Fig. 6) is very similar in details of shape to that of the Pratt Slide specimen (UNSM 100140) discussed above. Its measurements are: anteroposterior diameter of shaft at its broken end, 1.42 mm; transverse diameter of shaft at its broken end, 1.73 mm; transverse width of distal epiphysis, 2.86 mm. In size it matches the humerus of extant *Lasiurus ega* except that the shaft is stouter. In its stoutness it resembles a humerus referred by Thewissen and Smith (1987) to *Lasiurus fossilis*. Because of its generally similar age, the Big Springs specimen, too, might be referable to *L. cf. fossilis*. However, the species *L. fossilis* was originally based on a dentary with three teeth (Hibbard 1950); no postcranial bones certainly referable to the species are known

by direct association with jaws. The number of fossils of *Lasiurus* is slowly increasing across North America, but samples are not yet complete enough to determine how many different species occurred in the late Tertiary. In the meanwhile it seems prudent to be conservative in the identification of unassociated or fragmentary bones. Another extinct species, *Lasiurus golliheri* (Hibbard and Taylor 1960), is known from the late Pleistocene of Kansas, but its humerus is unknown.

The edentulous right dentary bone (UNSM 75993; Fig. 7A, B) is broken at the front and back of the jaw, but most of the horizontal ramus is preserved. Anteriorly it is broken through the alveolus for the lower canine. A mental foramen opens laterally on the ramus between the roots of the canine and anteriormost premolar. Three alveoli for lower premolar roots and six for molar roots are present.

Of North American vespertilionid bats of similar size having this postcanine alveolar formula (three premolar root sockets), the specimen most closely resembles *Nycticeius humeralis* and some species of *Lasiurus*. However, in *N. humeralis* there is less distance between the posterior alveolus of m3 and the anterior edge of the ascending ramus, the mental foramen is more anteriorly positioned, and the ventral edge of the ramus is less sinuous. Different species of *Lasiurus* have different numbers of premolar alveoli. In *Lasiurus cinereus*, the p4 is single-rooted, whereas in red bats (e.g., *Lasiurus blossevillii*, *L. borealis*, *L. seminolus*) and yellow bats (subgenus *Dasypterus*, e.g., *L. ega*, *L. intermedius*) the p4 is double-rooted. The p4 is also double-rooted in *L. fossilis*. The lower teeth and jaw of *L. (D.) golliheri* are unknown; the sole known specimen of the species being a maxilla fragment with C1-P4. The position of the posterior mental foramen and sinuosity and other details of dentary shape and alveolar sizes are similar to those of the type specimen of *L. fossilis*.

The alveolar tooth-row length from the anteriormost premolar alveolus to the posterior alveolus of m3 measures 4.6 mm in this edentulous jaw. By comparison, this measurement made on a few other specimens of *Lasiurus* is as follows: *L. fossilis*, 4.9 mm; *L. blossevillii teliotis*, 4.1 mm; *L. ega*, 5.1 and 5.5 mm (2 specimens); *L. cinereus*, 5.7 and 5.7 (2 specimens). In this measurement, then, the Big Springs fossil is closest to *L. fossilis*.

The third specimen from Big Springs is a fragment of right dentary (UNSM 54003; Fig. 7C–E). It preserves the m3, empty alveoli of m2, and a small portion of the ascending ramus. Broken edges of the specimen, except at the front, are somewhat abraded. On m3, the labial cingulum begins beneath the paraconid and ends abruptly lateral to the hypoconid. Hypoconulid is ab-

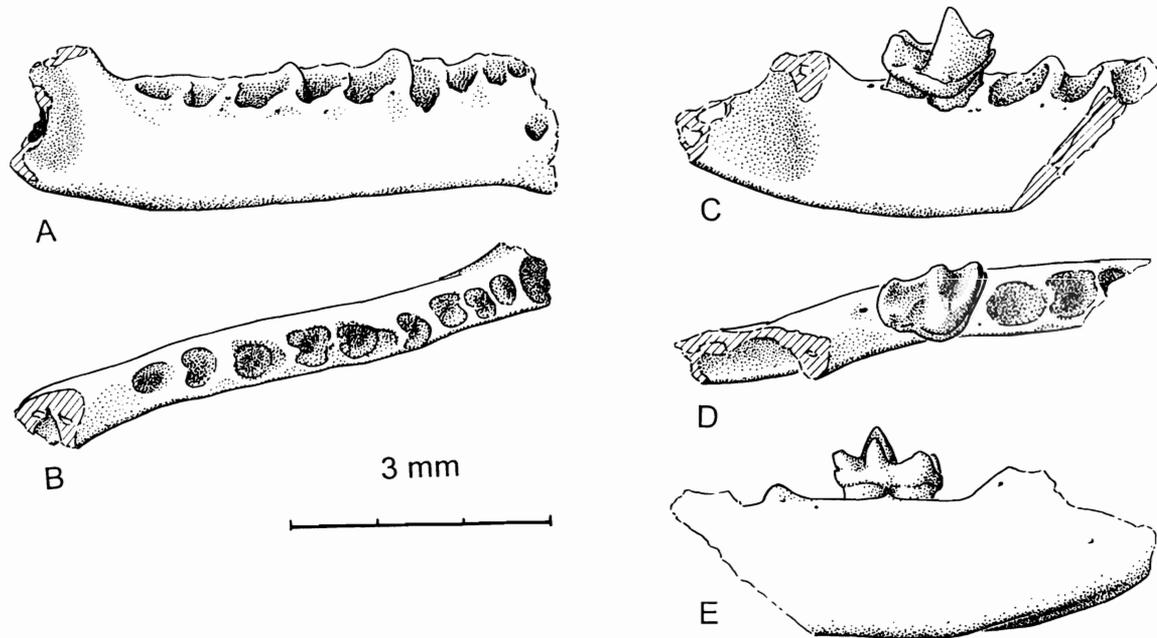


Figure 7. *Lasiurus* sp. indet. from UNSM locality Ap103. Edentulous fragment of right dentary (UNSM 75993) in A, labial and B, alveolar views. Fragment of right dentary with m3 (UNSM 54003) in C, labial, D, occlusal, and E, lingual views.

sent. Hypoconid and entoconid are moderately developed, rounded cusps that are not connected to each other by a cristid. A small rounded cristid extends forward from the entoconid. The cristid obliqua is rather low and rounded. Measurements of the specimen are: anteroposterior length of m3, 1.24 mm; transverse width of the trigonid of m3, 0.82 mm; transverse width of the talonid of m3, 0.56 mm; depth of the dentary below the protoconid of m3 (labial side), 1.27 mm; depth of the dentary below the anterior root of m3 on the lingual side, 1.40 mm.

In the characteristics described, the m3 most closely resembles that of the smaller extant species of *Lasiurus* (the m3 is unknown in the extinct species of *Lasiurus*). Unlike the Big Springs fossil, most other North American vespertilionid bats have a m3 with less reduced talonid possessing a weak to strong postcingulid and a weak to strong hypoconulid. Except for *L. cinereus*, modern specimens of *Lasiurus* species usually have a talonid configured like that of the fossil. By contrast, *Lasiurus cinereus* has a complete posterior cingulum, weak to strong hypoconulid, and postcristid connecting the hypoconid to the hypoconulid. Although the jaw fragment can be referred with some confidence to the genus *Lasiurus*, a specific determination is not possible. In size it approaches *L. fossilis* and *L. ega*.

DISCUSSION

If some of the Arikareean LMA specimens from Dw121 belong to *Myotis*, they would constitute the earliest record of the genus *Myotis* in North America, exceeding a Barstovian LMA (middle Miocene) occurrence of "cf. *Myotis*" from Antelope County, Nebraska (Czaplewski 1991), and Clarendonian LMA specimens from Kansas and Oklahoma (Wilson 1968, Dalquest et al. 1996). If they represent an undescribed genus or undescribed species of *Oligomyotis*, they would extend our understanding of the evolution of vespertilionid bats. Sadly, these "ifs" are moot until more complete specimens can be collected. Horáček (1994) noted that in Europe the Oligocene and early Miocene record of vespertilionids consists almost entirely of forms that have a *Myotis*-like dental pattern, but very few of them actually pertain to the genus *Myotis*. Even among the *Myotis*, the speciose nature of the genus and the minute morphological differences to be expected among *Myotis* and other vespertilionids during their initial radiations will continue to hamper our understanding of this widespread but interesting group of bats.

The Pratt Slide specimen represents the oldest record of a hairy-tailed bat (*Lasiurus*). It is some five to six million years older than a specimen from Idaho (a humerus attributed to *Lasiurus fossilis* that came from a site dating between 3.7 and 3.1 Ma; Thewissen and Smith 1987). It also exceeds a record of *Lasiurus* cf. *L.*

blossevillii from Arizona (Czaplewski 1993) by about five million years.

Given the overall paucity of fossil bat records in North America, it is difficult to generalize about the biogeographic or phylogenetic significance of these members of the Tertiary fauna. The earliest North American record of *Myotis* presented herein is exceeded by earlier records of the genus in Europe (early Oligocene of France; Revilliod 1919, 1922) and Asia (early-middle Oligocene of Kazakhstan; Gabunia and Gabunia 1987). Together these Paleogene records may indicate that the genus became widespread in northern continents within a few million years after it first evolved. *Myotis* has continued to maintain its dominance globally to the present day; it is currently one of the most species-rich genera of bats and one of the most widely distributed of all mammal genera.

Members of the genus *Lasiurus* appeared later—by the late Miocene—and have persisted into the Recent. Presently, they are widespread throughout temperate North and South America. Most species are solitary, tree-roosting bats that often utilize deciduous woods and woodlands bordering watercourses. They probably first evolved in woodlands and in riparian gallery forests that coursed through the grassy savannas that were widespread in the Great Plains by the mid-late Miocene (Gabel et al. 1998) and possibly elsewhere throughout the Americas during the mid-late Tertiary. The few fossil occurrences of *Lasiurus* known to date indicate that they spread widely through North America during the Pliocene.

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