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VESPERTILIONID BATS (CHIROPTERA, MAMMALIA) FROM THE PLIOCENE OF IDAHO

By

J. G. M. THEWISSEN AND G. R. SMITH

Abstract.—Remains of two bats, *Lasiurus* and *Antrozous*, are described from the Pliocene Glenns Ferry Formation of the Snake River Plain in southwestern Idaho. A humerus of *Lasiurus fossilis* was found in the lacustrine facies of the formation. A mandible of *Antrozous pallidus* was found in the stratigraphically higher fluvial facies, the Sand Point Local Fauna. The age of these remains is approximately 3 my. Pre-Pleistocene *Antrozous* was formerly known only from Texas, while pre-Pleistocene *Lasiurus* was known from Texas and Kansas.

INTRODUCTION

The Glenns Ferry Formation in the Snake River Plain of Idaho (Fig. 1) consists of Pliocene shoreface sands and offshore silts, overlain and surrounded by fluvial and floodplain sands (Malde and Powers, 1962; G. R. Smith et al., 1982). The upstream, fluvial and floodplain part of the formation has provided a wealth of fossil mammals (e.g. Gazin, 1933 and 1936; Hibbard, 1959; Hibbard and Zakrzewski, 1967; Zakrzewski, 1969; Bjork, 1970; Hibbard and Bjork, 1971; Shotwell, 1970), and is assigned to the Blancan Land Mammal Age.

Ongoing fieldwork by one of us (G. R. S.) is concentrated on the lower part of the Glenns Ferry formation, which is largely lacustrine in origin; large lakes ("Lake Idaho") covered much of the Snake River Plain of southwestern Idaho and southeastern Oregon in Miocene as well as Pliocene times (Kimmel, 1982; G. R. Smith et al., 1982). Fish remains are abundant in this part of the formation (Miller and Smith, 1967; G. R. Smith, 1975; G. R. Smith et al., 1982), while tetrapods are rare.

Bats are usually underrepresented in fossil mammal faunas, and are previously undescribed from localities of the Glenns Ferry Formation. Taylor (1966: p. 75, personal communication from C. W. Hibbard), lists the vespertilionid *Antrozous* as occurring in the Glenns Ferry Formation, but gives no description. We assume that this record refers to a specimen described here (UM 45151), a mandible with two teeth collected in 1962 by Hibbard and a University of Michigan field party at the Sand Point locality in Owyhee County, Idaho. In addition to this, we describe a bat humerus (UM 3298) from the lacustrine facies of the Glenns Ferry Formation. This specimen was collected by G. R. Smith and a University of Michigan field party in 1981, from Owyhee County, 5.1 miles WNW of the above locality.

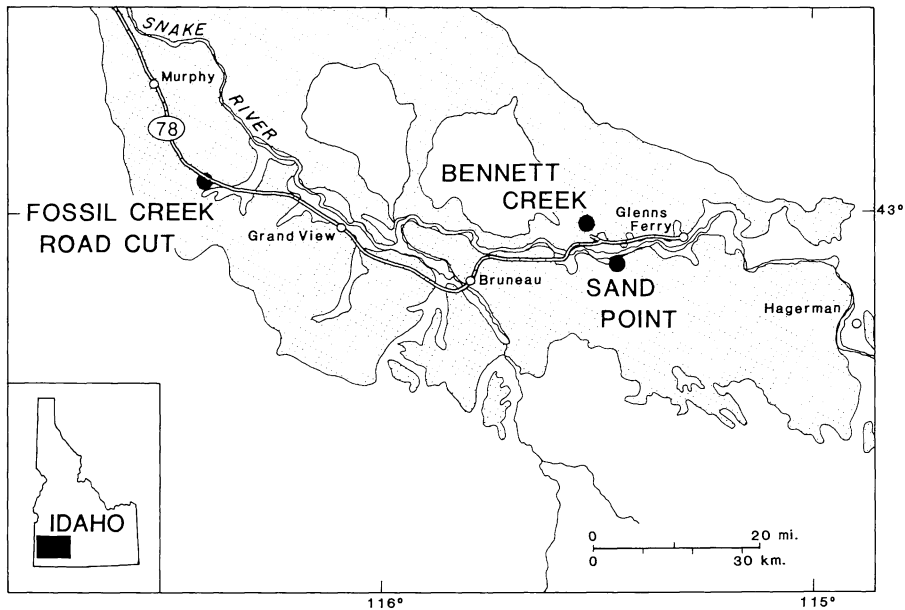


Fig. 1— Map of Snake River Plain of Western Idaho and Eastern Oregon. Extent of the Glenns Ferry Formation is hatched. “Fossil Creek Roadcut”: locality where UM 3298 was found. “Sand Point”, USGS Cenozoic localities 19128 and 19129, UM 45151 comes from beds below this locality.

METHODS

The terms used for anatomical directions are those that are conventional for mammals, and therefore do not coincide with the special positions that limb bones have in bats. Dimensions of teeth were measured with an ocular micrometer at an accuracy of 0.1 mm. Width of trigonid of lower molars is measured perpendicular to the long axis of the tooth, as the distance between the labial and lingual side of proto- and metaconid respectively. Width of the talonid of lower molars is measured perpendicular to the long axis of the tooth, as the distance between the labial and lingual sides of hypoconid and entoconid respectively.

We follow the chiropteran classification of Honacki et al., 1982.

Comparisons were made with many specimens in the University of Michigan Museum of Zoology (UMMZ) collections. The most relevant specimens were: Vespertilionidae, *Antrozous pallidus* (UMMZ 54294, 76283, and 93560); *Eptesicus furalis* (UMMZ 124449 and 125742); *E. fuscus* (UMMZ 30888 and 99293); *Lasionycteris noctivagans* (UMMZ 41285 and 156441); *Lasiurus borealis* (UMMZ 54118 and 89681); *L. ega* (UMMZ 125727 and 125728); *L. seminolus* (UMMZ 79812); *Miniopterus australis* (UMMZ 157121); *Myotis austroriparius* (UMMZ 99418); *M. californicus* (UMMZ 98964); *M. grisescens* (UMMZ 76868 and 106035); *M. keenii* (UMMZ 113201); *M. lucifugus* (UMMZ 106042); *M. myotis* (UMMZ 123523); *M. vivesi* (UMMZ 81155); *Nycticeius humeralis* (UMMZ 83902 and 83903); *Pipistrellus hesperus* (UMMZ 106128); *P. subflavus* (UMMZ 75662 and 76860); *Plecotus rafinesquii* (UMMZ 90975); *P. townsendii* (UMMZ 89991 and 90122); *Rhogeessa tumida* (UMMZ 116291 and 116297); *Scotophilus kuhli* (UMMZ 160311). Phyllostomidae, *Carollia brevicauda* (UMMZ 126806); *Macrotus waterhousii* (UMMZ 95717); *Micronycteris hirsuta* (UMMZ 125174); *Phyllostomus sp.* (UMMZ 56630). Molossidae: *Eumops*

bonariensis (UMMZ 125396); *E. perotis* (UMMZ 79576); *Molossops abrasus* (UMMZ 124450 and 125797); *M. temminckii* (UMMZ 125373 and 125374); *Molossus ater* (UMMZ 95671); *M. molossus* (UMMZ 95671); *Promops centralis* (UMMZ 125803); *P. nasutus* (UMMZ 124420); *Tadarida brasiliensis* (UMMZ 67243 and 79495). Mormoopidae: *Mormoops megalophylla* (UMMZ 116203); and *Pternotus parnellii* (UMMZ 105677).

SYSTEMATIC PALEONTOLOGY

Order CHIROPTERA

Family VESPERTILIONIDAE

Genus *Lasiurus* Gray, 1831

Lasiurus fossilis Hibbard, 1950

Figure 2

Referred specimen.—UM 3298 (right humerus).

Locality and age.—"Fossil Creek Roadcut" of the Fossil Creek Area (G. R. Smith et al., 1982); Eastside of highway 45, 2.5 miles SE of Fossil Butte, NE 1/4, S. 14, T4S, R1W, Western Idaho. The sediment of this locality consists of calcareous offshore sands. Based on biostratigraphic interpretation of the evolution of the teleost fish *Mylocheilus robustus* (G. R. Smith et al., 1982: fig. 6), the Fossil Creek localities are considered older than the Bennett Creek locality (SW 1/4, S. 16, T5S, R8E), which is in turn equivalent in age to the Sand Point locality (see below), as is indicated by chemical analysis of volcanic ashes (ashes "Bennett 42" and "Sand Point 43", Swirydczuk et al., 1982). The Sand Point locality, with the Sand Point Local Fauna, is considered middle Blancan Land Mammal Age, approximately 3.1 my (Repenning, pers. comm.). This date coincides well with two fission track dates from the two ashes, between which the Fossil Creek Localities are situated (Kimmel, 1982), they yield 3.3 +/- .4 (ash layer 77-4) and 2.5 +/- .2 my (ash layer F2). Due to the regressive nature of the sequence, the younger ash is lower in elevation than the older one (Kimmel, 1982: table 1; Smith et al., 1982: table 1; and Swirydczuk et al., 1982: fig. 11). These dates allow us to estimate that the Fossil Creek Roadcut locality is between 3.1 and 3.7 my b.p.

Description.—The humerus (Fig. 2) is 30.0 mm long, proximally 3.6 mm wide (measured between the tubercles) and the width of the condyle is 2.3 mm (measured at the most distal point).

The humeral head is ovoid, its longest axis runs latero-distally, and convexity is strongest in its lateral third. The articular surface has a triangular expansion on the greater tubercle.

A broad notch separates the head from the greater tubercle. The latter projects farther proximally than the lesser tubercle and head. A ridge connects the greater tubercle to the pectoral crest. The lateral head of the triceps originates partly from the concave lateral side of the pectoral crest, and from a rugose area latero-distal to the pectoral crest. A ridge, marking the boundary of the origin of the lateral head (Norberg, 1970; Vaughan 1970) runs from the caudal part of this rugose area proximally, bending medially and ending at the distal part of the humeral head. The medial part of the pectoral crest is also concave, forming a smooth area over which the biceps runs. In anterior view the pectoral crest tapers distally, it reaches its highest point at 5.0 mm from the proximal extremity of the bone, and disappears just distal to that.

The proximal part of the pectoral crest is connected to the lesser tubercle by a ridge. This ridge, the ridge connecting the pectoral crest to the greater tubercle, and the humeral head form the edges of a deep basin in the proximal extremity of the humerus. The lesser tubercle is lower than the humeral head, and a ridge runs distally from it. This ridge ("medial ridge" of Vaughan, 1959) has its highest

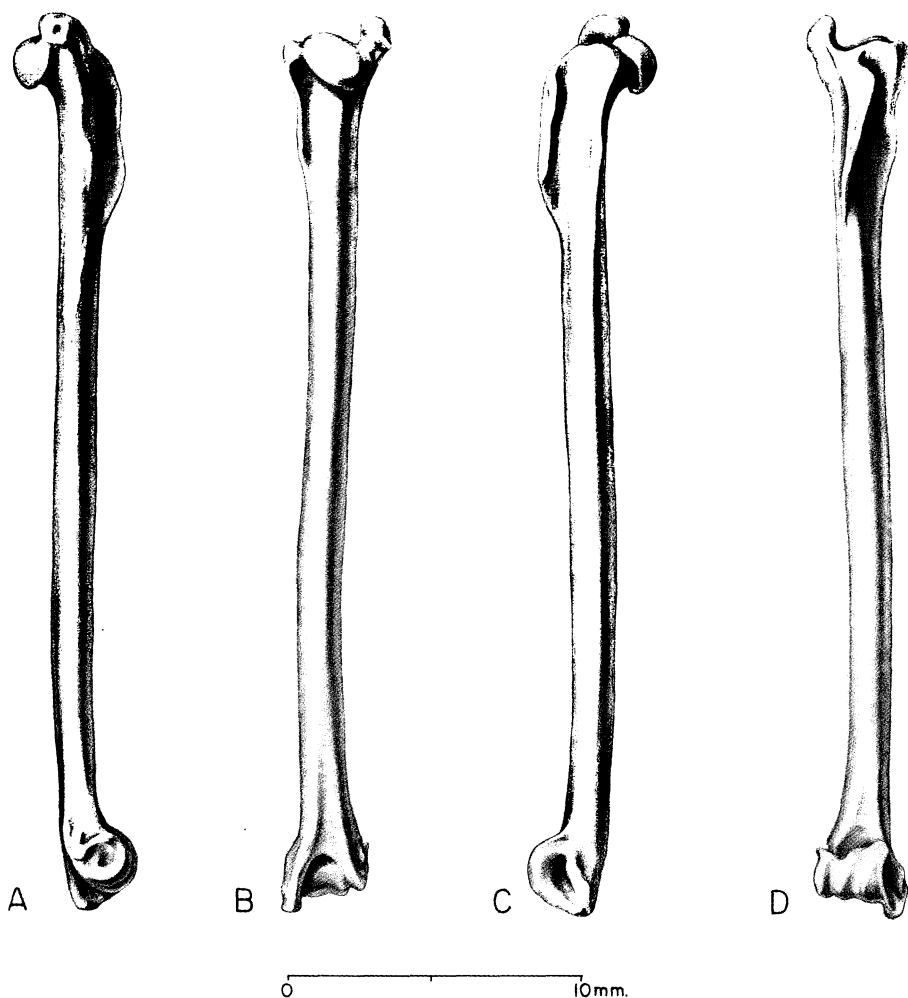


Fig. 2— *Lasiurus fossilis*, right humerus (UM 3298; A, lateral view; B, posterior view; C, medial view; D, anterior view).

point at 3.4 mm from the proximal extremity of the lesser tubercle. Its caudal part and the adjacent part of the humeral neck are concave. Part of the lateral head of the triceps originates from this area (Norberg, 1970; Vaughan, 1970).

A shallow depression is present proximal to the trochlea on the anterior side. The trochlea extends further proximal than the capitulum, both anteriorly and posteriorly. Its axis is somewhat oblique with respect to the bone. Medially it forms a broad flat area, and laterally a wide ridge extends over the whole length of the condyle, marking the boundary with the capitulum. The capitulum has another ridge on its lateral side. A small projection of the capitulum occurs on a bony process of the lateral epicondyle, pointing proximo-laterally.

The lateral epicondyle has a shallow groove just proximal to the condyle, for the origin of the short and long extensor carpi radialis. A deep pit occurs distal to it in the middle of the epicondyle. The supinator originates from it (Norberg, 1970; Vaughan, 1970).

The medial epicondyle has a deep depression in its center, bounded posteriorly by a steep wall. A strong ligament originates from it and the postero-distal part of the medial epicondyle is elongated,

forming a process for the origin of flexor carpi ulnaris. The lateral wall of this process has an elongated concavity, which is directly adjacent to the trochlea. Proximal to the trochlea, the concavity bends lateral and ends at the most proximal part of the condyle.

Discussion.—Bat humeri are of considerable taxonomical interest (e.g. Revilliod, 1922; Lawrence, 1943; Vaughan, 1959; Legendre, 1982). J. D. Smith, 1972, described New World bat humeri in detail. Using characters from his work, we identify UM 3298 as being either a molossid or a vespertilionid: the greater tubercle projects far more proximally than the head (also in Phyllostomidae, but not in Mormoopidae); the condyle is not laterally displaced (in contrast to Phyllostomidae and Mormoopidae); the medial epicondyle has a distally projecting process, and lacks a medial projection (as in some Vespertilionidae, all Molossidae and Mormoopidae, but not in Phyllostomidae); and a locking mechanism for the scapula is present on the greater tubercle (in contrast to Mormoopidae).

A number of differences between vespertilionids and molossids were cited by J. D. Smith (1972), but exceptions are present for all characters and only in combination do these make it possible to distinguish between the families and genera.

UM 3298 has an elongated head, a characteristic that occurs in many molossids and in some vespertilionids (J. D. Smith, 1972). It is comparable in this feature to the vespertilionid *Lasiurus* and the molossids *Molossus*, *Promops*, and *Tadarida*.

The greater tubercle projects well beyond the humeral head in UM 3298. Usually these are subequal in vespertilionids, while molossids have a more projecting greater tubercle. The fossil specimen resembles the vespertilionids *Lasiurus*, *Myotis*, and *Pipistrellus*, the molossids *Tadarida*, and some species of *Molossops*.

The depression in the proximal extremity of the humerus is usually deep in molossids and shallow in vespertilionids. UM 3298 is comparable to *Lasiurus* and all studied molossids.

The pectoral crest is usually more lateral in molossids than in vespertilionids, this can be observed when the bone is oriented in the plain between the two tubercles. UM 3298 resembles the vespertilionids *Antrozous*, *Lasionycteris*, *Lasiurus*, *Nycticeius*, *Pipistrellus*, *Plecotus*, and *Rhogeessa*, and the molossids *Molossus* and *Promops*.

The capitulum of molossids is usually wider than in vespertilionids. For the studied species of the two families, the ratio capitulum width/condyle width (both measured at the distal extremity), ranged from .30 to .41 in vespertilionids, and from .41 to .46 in molossids. In UM 3298 the ratio is .33, which is intermediate between *Lasiurus ega* ($n = 4$; mean = .336; s.d. = .023) and *Lasiurus borealis* ($n = 4$; mean = .323; s.d. = .012).

The postero-lateral side of the medial epicondyle has a deep groove in UM 3298 ("pocket-like olecranon fossa" of Lawrence, 1943). A similar groove is found in the vespertilionids *Miniopterus* and *Lasiurus*, but not in other vespertilionids or molossids.

The distally projecting process of the medial epicondyle projects beyond the trochlea in UM 3298. A similar sized process is present in the vespertilionid *Lasiurus*. It is much stronger in molossids and *Miniopterus* while it does not project beyond the trochlea in other vespertilionids.

The medial epicondyle has a deep concavity in UM 3298, *Lasiurus* and molossids, but not in other vespertilionids, in which it is either shallow or completely absent.

On basis of the cited characters we refer UM 3298 to the genus *Lasiurus*. We consider the four characters of the distal humerus as the most diagnostic. Seven species of *Lasiurus* are known from the continental United States (Hall, 1981; Martin, 1972). *Lasiurus cinereus* (Late Pleistocene - recent, Martin, 1972) is the only species that ranges into southwestern Idaho, but the described humerus is too large to pertain to it. *Lasiurus borealis*, although not known to occur in Idaho, is widely distributed in the temperate regions of North America: it is smaller than UM 3298. The other extant species of *Lasiurus* do not range into the northwestern region of the U.S., although the fossil humerus compares in size well with *L. ega* and *L. seminolus*. Two species of *Lasiurus* are only known through fossils: *L. gollitheri* (Hibbard and Taylor, 1960) occurs in the Late Pleistocene of Kansas and *L. fossilis* Hibbard,

1950, is known from the Late Pliocene of Kansas. No direct comparison between these is possible, since no element is known for both species. The holotype of *L. fossilis* (UM 25763, dentary with P₄-M₂) differs morphologically from all extant species of *Lasiurus* in having a weaker paraconid (especially on M₁), more open trigonids, weaker cingulae and more obtuse cusps. Hibbard, 1950, and Hall and Jones, 1961, consider this species ancestral to *L. cinereus*.

On basis of the only evidence available for specific identification, size and age, we refer UM 3298 to *L. fossilis*.

Genus *Antrozous* H. Allen, 1862
Antrozous pallidus Le Conte, 1862
 Figure 3

Referred specimen.—UM 45151 (partial left dentary with M₂ and M₃).

Locality and age.—Stratigraphically below USGS Cenozoic localities 19128 and 19129: S 1/2, SW 1/4, S. 1, T6S, R8E; a promontory south of the Snake River, southeast of the town of Hammett, Owyhee Countee, Idaho. This locality yields specimens from the Sand Point Local Fauna (see faunal list in Hibbard, 1959) and is considered intermediate between the early Blancan Hagerman and the late Blancan Grand View Local Faunas (Bjork, 1970; Neville et al., 1979). According to Repenning (pers. comm.) the Sand Point Local Fauna represents the middle Blancan Land Mammal Age, and is approximately 3.1 my old. Paleomagnetic evidence from the Sand Point ash show that the Sand Point localities are in the earliest Matuyama Normal or one of the two normal events of the Gauss Reversed (Neville et al., 1979, p. 518), i.e. between 2.2 and 3.2 my (Berggren et al., 1985).

Description.—The mandible (Fig. 3) preserves the posterior part of the posterior alveolus for M₁, part of the ascending ramus and masseteric fossa. The trigonid of M₂ is worn and the protoconid broken off, but the latter was certainly much higher than paraconid and metaconid, protoconid and metaconid are well developed. The entoconid is placed on the lingual edge of the tooth and a strong crest runs anteriorly from it, reaching the posterior side of the metaconid. The hypoconid and entoconid are connected by a strong crest, and the cristid obliqua touches the trigonid just medial to the protoconid. A strong cingulum is present on the anterior side of the tooth; it descends the tooth labially. It is continuous along the whole labial border of the tooth and ascends the tooth again posteriorly, ending at the most lingual edge in a small cusp, the hypoconulid.

The trigonid of M₃ is unworn and undamaged, and similar in morphology to that of M₂. The talonid is strongly reduced, and the hypoconid and entoconid are close. The cristid obliqua and the preentocristid are low and run both to the posterior side of the metaconid. The anterior cingulum is well developed, but on the labial side the cingulum narrows while running alongside the trigonid, and it lacks on the posterior side.

Discussion.—UM 45151 resembles the studied vespertilionids, but not phyllostomids, molossids, and mormoopids, in that it has a distinct hypoconulid on M₂, which is well set off from the entoconid. It resembles phyllostomids such as *Macrotus* and *Phyllostomus* and the mormoopid *Mormoops* in the reduced condition of the talonid of M₃, without the trigonid being significantly smaller than M₂. The talonid of these taxa is more elongated than in UM 45151, however. Among vespertilionids, M₃ talonid reduction occurs in *Eptesicus* and *Antrozous*. UM 45151 matches closely with the latter genus. This feature can be quantified by the ratio width of trigonid/width of talonid. In UM 45151 this index is 1.8, in *Antrozous pallidus* the mean is 1.90 (n = 15, s.d. = .24) and in *Eptesicus fuscus* 1.41 (n = 10, s.d. = .12).

The fossil specimen matches in size (Table 1) and shape *Antrozous pallidus*, the only species of

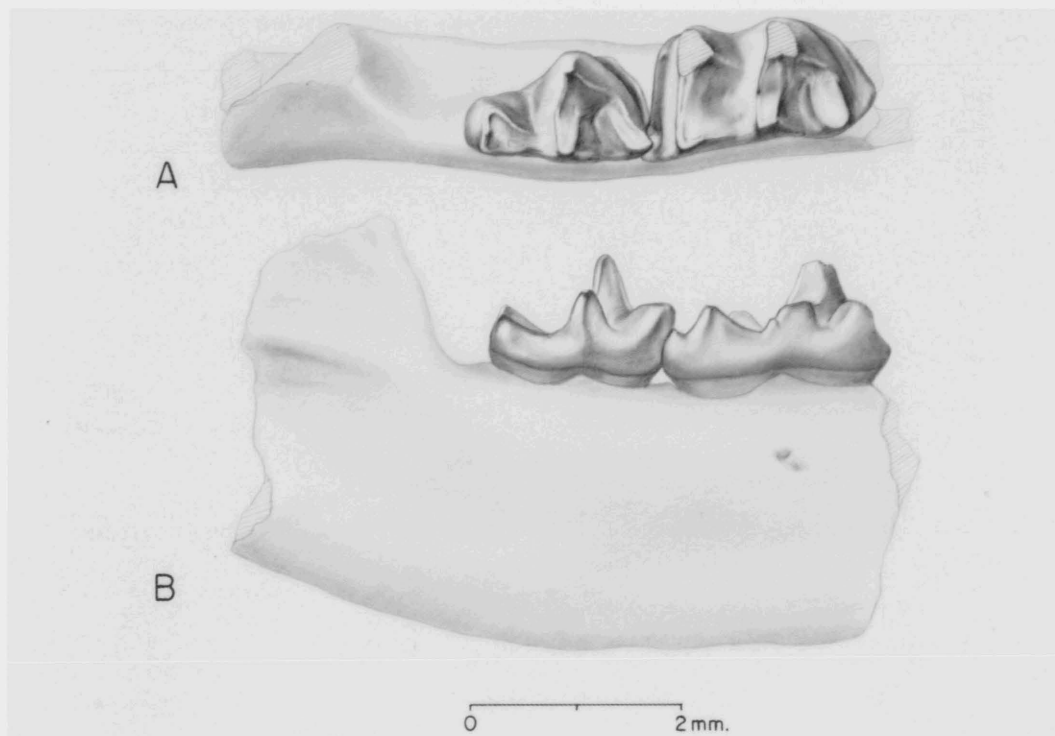


Fig. 3— *Antrozous pallidus*, left dentary with M₂, M₃. (UM 45151; A, occlusal view; B, lingual view).

Antrozous that occurs in the temperate regions of North America. On the basis of this resemblance, we refer UM 45151 to *Antrozous pallidus*.

UM 45151 resembles closely *Anzanycteris anzensis* White, 1969 from the late Blancan of California. According to the type description of this taxon, it differs only in details of the lower incisors from *Antrozous pallidus*, and is indistinguishable in the molars.

CONCLUSIONS

Pliocene *Antrozous pallidus* was formerly only known from the Beck Ranch Local Fauna of Texas (Dalquest, 1978). The humerus of *Lasiurus fossilis* is the first record of the species in Idaho, and it is the first postcranial element known.

Recent temperate species of *Lasiurus* are tree roosters, migrating south before winter. Fossil *Lasiurus*, now known from Idaho and Kansas, indicate that this habit is probably at least 3 million years old. Recent *Antrozous* are cavernicolous that hibernate.

Few late Tertiary vespertilionids are known, and they have been described as being similar to modern *Eptesicus* (Stirton, 1931; Lawrence, 1943; Shotwell, 1970; Dalquest, 1978), *Eptesicus* and *Myotis* (Sutton and Genoways, 1974), *Lasionycteris* (Dalquest, 1978), or *Miniopterus* (Hall, 1930). The resemblance of Late Tertiary vespertilionids to extant taxa indicates that radiation of the family was completed by Pliocene times.

TABLE 1 — Measurements on Pliocene and Recent *Antrozous pallidus* (in mm). W.tri. : width of trigonid. W.tal. : width of talonid.

Dimension	Pliocene <i>A. pallidus</i> (UM 45151)		Recent <i>A. pallidus</i> (n = 15)			
	M ₂	M ₃	M ₂		M ₃	
			mean	s.d.	mean	s.d.
Length	1.7	1.9	2.04	.12	1.74	.13
W.tri.	1.2	1.1	1.18	.13	1.11	.07
W.tal.	1.3	.6	1.29	.12	.59	.08

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