A new species of bat (Chiroptera: Vespertilionidae) from the early Oligocene global cooling period, Brule Formation, North Dakota, USA

Nicholas J. Czaplewski[a]*, Jeff Person[b], Clint Boyd[b] & Robert J. Emry[c]

[a] Oklahoma Museum of Natural History, 2401 Chautauqua Avenue, University of Oklahoma, Norman, OK 73072, USA
[b] North Dakota Geological Survey, 600 East Boulevard Avenue, Bismarck, ND 58505, USA
[c] Department of Paleobiology, United States National Museum of Natural History, Smithsonian Institution, NBH MRC 121, Washington, DC, USA
* Corresponding author: nczaplewski@ou.edu

Abstract: We report the first confirmed fossil bats from North Dakota, including a new species referable to the Vespertilionidae represented by a maxilla with P4-M3 from the Brule Formation, Fitterer Ranch local fauna, early Oligocene, Whitneyan North American Land Mammal Age. Unassociated postcranial fragments of the humerus and femur also represent a vespertilionoid, but appear to reflect a different, unidentified species. The new taxon, *Quinetia frigidaria* sp. nov., is referred to the genus *Quinetia*, previously known only from approximately contemporaneous deposits in Europe. The new species is larger than *Quinetia misonnei* from the early Oligocene of Belgium. It is similar in some morphological characters to *Chadronycteris rabenae* (Chiroptera incertae sedis) of the late Eocene (Chadronian) of northwestern Nebraska and to *Stehlinia* species (?Palaeochiropterygidae) from the Eocene and Oligocene of Europe, but differs from each in morphological details of the dentition and maxilla. An unassociated talonid of a lower molar from Fitterer Ranch shows myotodont morphology, unlike the nyctalodont lower molars in *Q. misonnei*, and thus represents a second chiropteran taxon in the fauna. *Quinetia frigidaria* is a member of a Paleogene radiation of bats near the low point of the Eocene-early Oligocene decline in global temperatures, increased seasonal aridity, and loss of tropical floras from mid-latitude North America.

Keywords: Mammalia, Plecotini, *Quinetia*, Oligocene, Eocene-Oligocene global cooling

INTRODUCTION

The mammalian order Chiroptera is the second most diverse order of mammals today (after Rodentia), and had its origins probably in the early Paleocene (Teeling *et al.*, 2012; Shi & Rabosky, 2015; Simmons & Cirranello, 2018; Lei & Dong, 2016). With a fossil record currently extending only back to the early Eocene, bats' initial diversification resulted in several archaic families and forms represented by fossils in several continents and subcontinents (Smith *et al.*, 2012). Fossil-calibrated molecular phylogenetic evidence suggests that crown-group bats had appeared and diversified by late Paleocene, while a few crown-group bat fossils first appear in Eocene and Oligocene rocks (O'Leary *et al.*, 2013; Smith *et al.*, 2012; Gunnell *et al.*, 2017). Among these were the Vespertilionoidea (Simmons *et al.*, 2008; Hand *et al.*, 2016). One vespertilionoid family, the Vespertilionidae, is the most speciose bat family in the present day (Simmons, 2005; Shi & Rabosky, 2015; Simmons & Cirranello, 2018). Information about the Paleogene and later radiation of the Vespertilionidae is scattered, their fossil record is relatively weak and limited largely to teeth and jaw fragments, which in the early forms exhibit a great deal of intractable morphological conservatism (e.g., Ziegler, 2000; Horácek, 2001; Eiting & Gunnell, 2009; Gunnell *et al.*, 2012; Maitre, 2014; Gunnell *et al.*, 2017). In addition, the earth underwent a pronounced climatic cooling during the Eocene-Oligocene transition, with a precipitous drop in the early Oligocene (Sheldon & Retallack, 2004; Pearson *et al.*, 2007; Zanazzi *et al.*, 2007; Zachos *et al.*, 2008; Liu *et al.*, 2009) that probably affected the evolution of bats and other organisms.

Oligocene fossils of bats in North America are few. In the late Eocene of North America, two putative vespertilionoids of uncertain family, *Chadronycteris rabenae* Ostrander, 1983 and ?*Stehlinia* sp., provide records of bats from northwestern Nebraska of the Chadronian North American Land Mammal Age (NALMA; Ostrander, 1983, 1985, 1987). *Chadronycteris* is unique to North America, while the genus *Stehlinia* Revilliod, 1919 is widely known by several species in European localities from middle Eocene to late Oligocene (Sigé, 1974, Sigé & Legendre, 1983; Crochet *et al.*, 1981; Smith *et al.*, 2012; Maitre, 2014). Bats previously reported from the early Oligocene of North America include an unidentified vespertilionid from the late Orellan of southwestern Montana (Tabrum *et al.*, 1996), and another vespertilionid, *Oligomyotis casementi* Galbreath, 1962, from the Orellan of northeastern Colorado, represented by a single distal humerus (Galbreath, 1962). In the late Oligocene, Storer (2002) reported an M1 or M2 from the early Arikareean Kealey Springs local fauna (Eastend area), Saskatchewan, that he described as a vespertilionoid similar to *Chadronycteris*. Other late Oligocene bats in North America include ?*Oligomyotis* or ?*Myotis* from the early Arikareean NALMA of northwestern Nebraska (Czaplewski *et al.*, 1999) and diverse bats from Florida, USA, in faunas of the Whitneyan and early Arikareean NALMAs, including members of the families Emballonuridae, Mormoopidae, Natalidae, Molossidae, and Speonycteridae (Czaplewski *et al.*, 2003; Morgan & Czaplewski, 2003; G. S. Morgan & N. J. Czaplewski, unpubl. data; Czaplewski & Morgan, 2012; Morgan *et al.*, 2019).
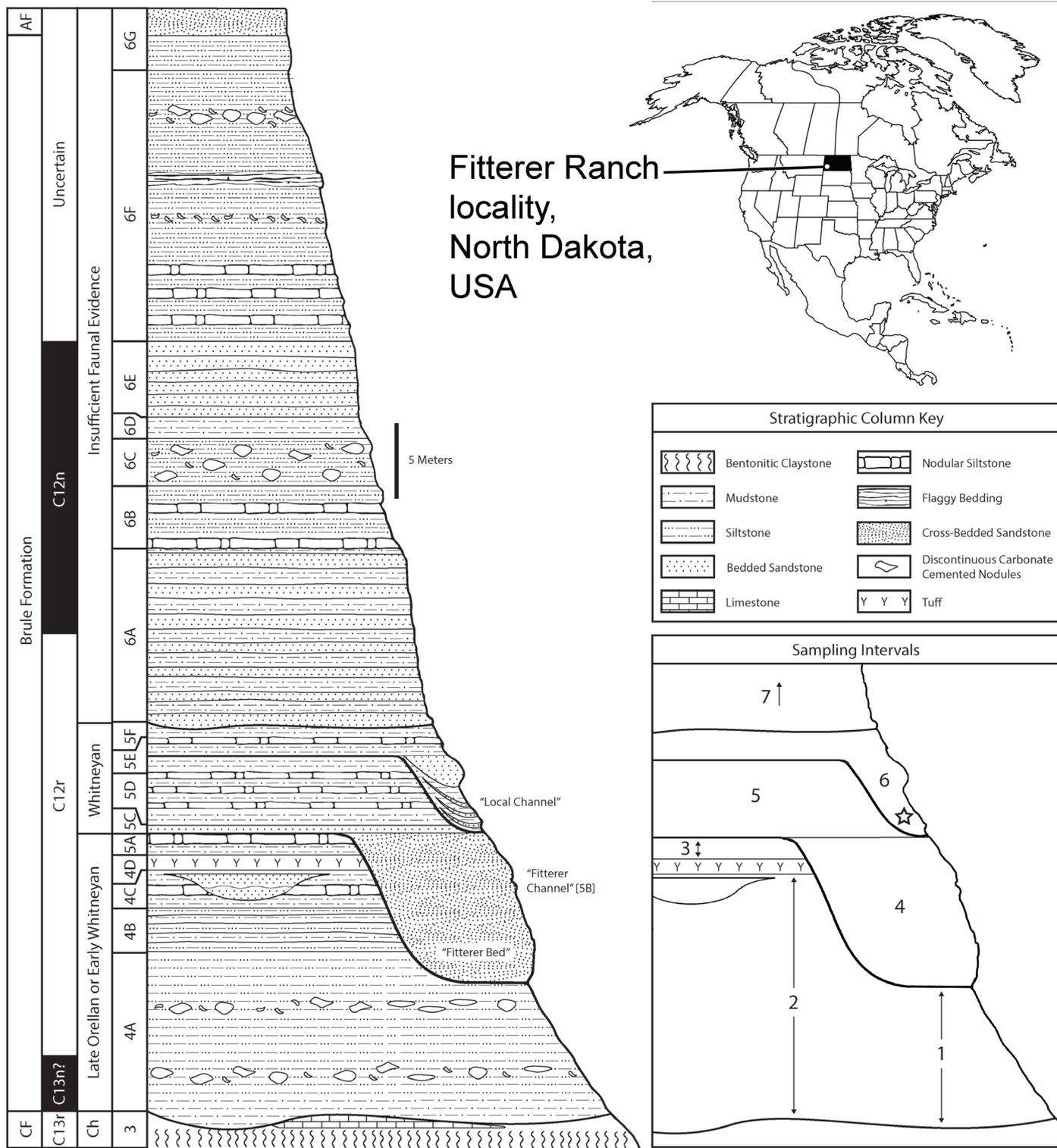
Figure 1. Generalized stratigraphic column for the Fitterer Ranch area of Stark County, North Dakota. Stratigraphic data derived from personal observations of the authors, unpublished field notes of Richard H. Tedford (provided courtesy of the American Museum of Natural History), and published data (Skinner, 1951; Stone, 1973; Murphy *et al*., 1993). On the left-hand side of the stratigraphic column are, from left to right, the formations, the magnetostratigraphic data of Prothero (1996: fig. 5), the North American Land Mammal Ages (NALMAs) inferred from this study, and the numbered lithostratigraphic units and sub-units defined by Skinner (1951) and their boundaries. Geographic location of North Dakota (black) showing the Fitterer Ranch study area (white dot within black) shown in upper right inset map of North America. A key to lithologies and sedimentary structures is provided in the center right. The lower right inset details the stratigraphic ranges of the seven "sampling intervals" defined in Korth et al. (2019), with a star indicating the position of the chiropteran specimens described in this study; note that these sampling intervals are numbered differently from Skinner's (1951) lithostratigraphic units, and that the placement of the bat-bearing local channel in Unit 5E differs from Skinner's (1951) placement of the same channel at the base of Unit 6A. Abbreviations: AF, Arikaree Formation; C, Chron; CF, Chadron Formation; Ch, Chadronian NALMA; n, normal polarity; r, reverse polarity.

Herein we report several vespertilionid fossils of early Oligocene age from the Brule Formation at the Fitterer Ranch locality, Stark County, North Dakota (Fig. 1). The main Fitterer Ranch samples are from the lower part of the Brule Formation (units 4 to 6A of Skinner [1951]) and have yielded a fauna and flora of early Oligocene age (Fig. 1). Hoganson & Lammers (1985, 1992) interpreted the diverse fauna and flora from the Brule Formation of southwestern North Dakota as being savanna-adapted with taxa potentially representing riparian gallery woodland, open savanna, and shallow pond communities. The reported vertebrate fauna of the Brule Formation within North Dakota is largely based on preliminary faunal lists presented without detailed discussion (e.g., Hoganson & Lammers, 1985, 1992; Kihm & Lammers, 1986). An effort is underway to refine our knowledge of that fauna, including a thorough review of the microvertebrates collected in the Little Badlands area (Stark County, North Dakota) and held in the North Dakota State Fossil Collection. Although specimens were referred to Chiroptera from the lower part of the Brule Formation of this area by Hoganson & Lammers (1985, 1992) and by Kihm & Lammers (1986), no detailed descriptions or discussion of those specimens were accomplished until now

Biostratigraphy of the Brule Formation and Depositional Context at the Fitterer Ranch

The fauna of the Fitterer Ranch has been considered Orellan or Whitneyan (Hoganson & Lammers, 1985, 1992; Hoganson et al., 1998; Janis et al., 2008: appendix 1). A recent study of the rodent assemblage at Fitterer Ranch divided the Brule Formation into seven stratigraphically stacked "sampling intervals" (not equivalent to Skinner's [1951] lithostratigraphic units) and assessed the age of the fauna preserved in each sampling interval (Korth et al., 2019). The fauna recovered from the lower (older) sampling intervals (1-3) was considered to be transitional Orellan/Whitneyan or Whitneyan, while the upper sampling intervals (4-7) preserved a clearly Whitneyan fauna. Biochronologically informative rodent taxa found in sampling intervals 4-7 include the castorid *Agnotocastor praetereadens* Stirton, 1935, the heliscomyid *Heliscomys medius* Korth, 2007, and the sciurid *Hesperopetes jamesi* Emry & Korth, 2007, which are elsewhere restricted to the Whitneyan (Prothero & Emry, 2004; Korth, 2010, 2014). The cricetid *Eumys brachyodus* Wood, 1937 is the most abundant rodent taxon found in all sampling intervals at Fitterer Ranch (Korth et al., 2019) and is reported from Whitneyan through early early Arikareean faunas (Black, 1961; Swisher, 1982; Tabrum et al., 1996; Tedford et al., 2004; Korth, 2010, 2014). Specimens previously referred to *E. brachyodus* from the Orellan Cook Ranch local fauna in Montana are now referred to *Eumys cricetodontoides* (Korth, 2019). In addition to the evidence provided by the rodent taxa, the oreodonts *Miniochoerus starkensis* Schultz & Falkenbach, 1956 and *Merycoidodon bullatus* Leidy, 1869 are both present in sampling intervals 1-6 and elsewhere co-occur only during the latest Orellan and early Whitneyan NALMAs (Prothero & Emry, 2004). The bat specimens under study were recovered from a "bone breccia" within sampling interval 6 of Korth et al. (2019); the site occurs in the local channel at the base of Unit 6A of Skinner's (1951) published section, although some of us (Boyd, Person) believe that this local channel actually cuts down from within Skinner's Unit 5E, as indicated in Figure 1. Thus, the bats were part of a Whitneyan fauna, although the data to resolve whether they are from the early or late Whitneyan are unavailable at this time. This new occurrence extends the geographic and biostratigraphic range of early vespertilionids, and fills an important gap in our current understanding of early chiropteran evolution.

The local channel fill that produced the bat specimens occurs within a substantially larger-scale channel fill deposit. The larger channel fill sequence has thick beds of coarse channel sandstones, indicating through-going, active streams. So at least some of the faunal elements preserved in this channel fill sequence would represent a riparian habitat. The "bone-breccia" bed that produced these bat specimens, as well as most of the small rodents described in Korth et al. (2019), is also rich in remains of freshwater gastropods, fishes, anuran amphibians, lizards, snakes, small birds, and many kinds of small mammals not yet studied, and fragmented specimens of larger mammals such as *Leptomeryx*, *Mesohippus*, and others. The bones occur as individual elements, with no articulation or association.

METHODS

The Fitterer Ranch bat specimens were recovered by two methods: by acid preparation from blocks of richly fossiliferous, carbonate-cemented sandstone collected in 1978 and 1983 from limited, small-scale, meandering, ribbon-like beds in the base of Skinner's Unit 6A (USNM specimens; Skinner, 1951) and by screenwashing of the same deposit (NDGS specimen; stratigraphic position reinterpreted herein as at the center of Skinner's Unit 5E; Skinner, 1951). None of the specimens were found in association.

The dental terminology used here follows Simmons et al. (2016), Gunnell et al. (2017), and Ravel et al. (2016) and the postcranial terminology follows Vaughan (1959), Gunnell et al. (2015), Amador et al. (2018), and Louzada et al. (2019). Specimens were examined on an Olympus SZX9 stereomicroscope, measured with an ocular micrometer calibrated with a micrometer slide, and drawn with a camera lucida attachment. The maxilla NDGS 1691 was also photographed in iterative series and in stereo using a digital single lens reflex camera with bellows and StackShot automated focus stacking rail and driver; the resulting images were prepared using Helicon Focus focus-stacking and Adobe Photoshop software. We estimated body mass of the extinct taxon using equations generated from least squares linear regressions for measurements of the teeth and body weights of modern bats (Czaplewski & Gordon, 2005 and unpubl. data).

Abbreviations: Ar, Arikareean; NALMA, North American Land Mammal Age; NDGS, North Dakota Geological Survey, Bismark; Or, Orellan; SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City; USNM PAL, Department of Paleobiology, United States National Museum of Natural History, Washington, D.C.; Wh, Whitneyan.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Chiroptera Blumenbach, 1779
Suborder Yangochiroptera Koopman, 1985
Superfamily Vespertilionoidea Weber, 1928
Family Vespertilionidae Gray, 1821
Tribe Plecotini Gray, 1866
Genus *Quinetia* Horácek, 2001
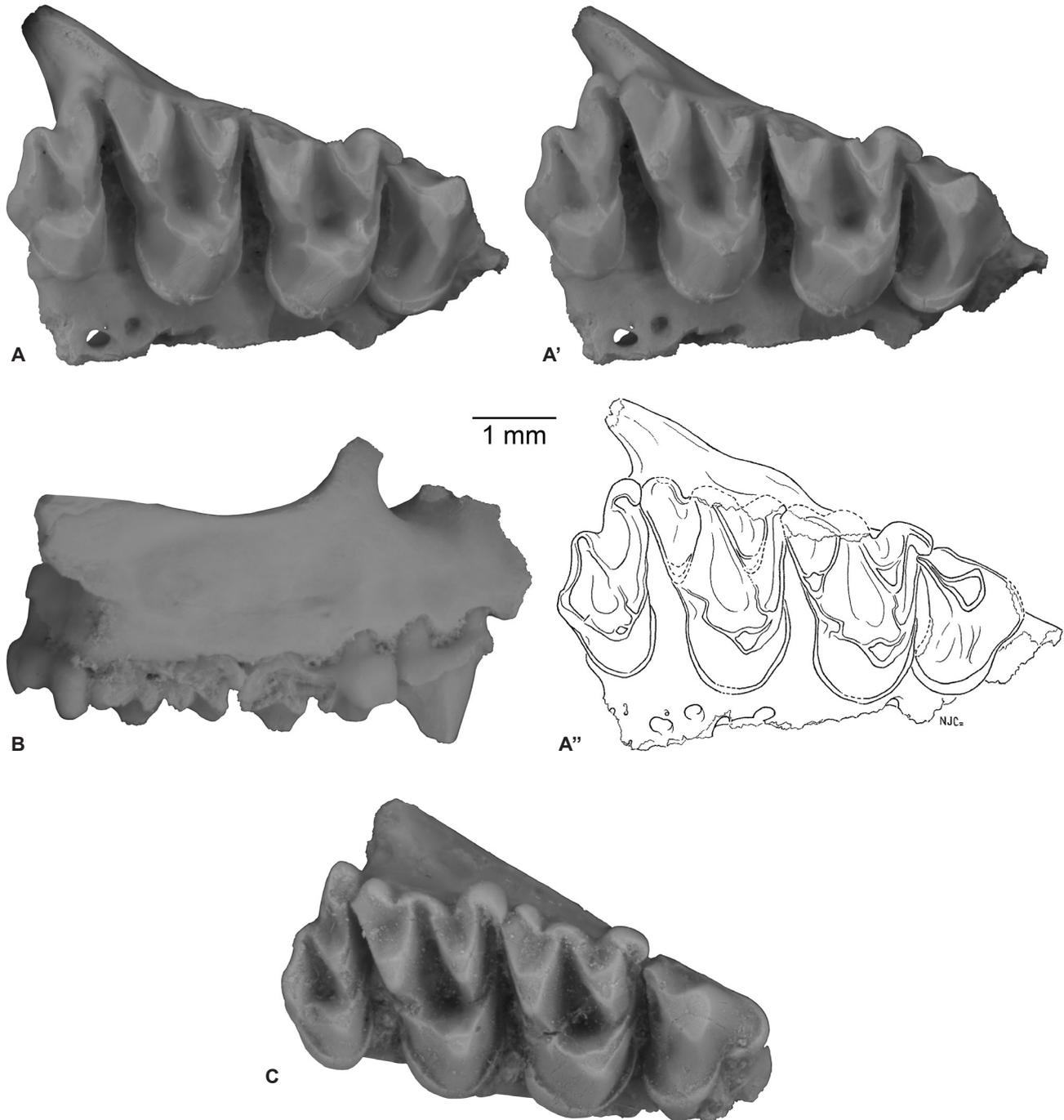
Quinetia frigidaria n. sp.

lsid:zoobank.org:act: 1CF8F35D-AF7D-44BF-8A3E-F39D84BE85F9

Figure 2, Table 1

Holotype and only known specimen: NDGS 1691, right maxilla with P4-M3, anterior root of zygomatic arch, orbital floor, and part of infraorbital canal.

Diagnosis: Medium-sized vespertilionid bat with very short infraorbital canal, with the upper molars lacking hypoconal shelves and hypocones, mesostyles projecting at the labial edge of the molars, relatively deep, narrow anterior and posterior ectoflexids, low but distinct paraconules and metaconules and distinct conular crests (postmetaconular crests are truncated). Differs from *Quinetia misonnei* (Quinet, 1965) in larger size. Differs from *Stehlinia* in having a much shorter infraorbital canal, in lacking a mid-labial vertical crest on P4, in having wider and shorter M1 and M2, in having more reduced hypoconal shelves on M1 and M2, and less prominent metaconule on M1 and M2. Differs from *Chadronycteris* in having a shorter infraorbital canal, less pronounced anterior

Figure 2. Maxillae of *Quinetia frigidaria* n. sp., from Fitterer Ranch, North Dakota, Brule Formation, early Oligocene, and *Chadronycteris rabenae* from Raben Ranch, Nebraska, Chadron Formation, late Eocene. **A** and **A'**, *Quinetia frigidaria*, NDGS 1691, right maxilla with P4-M3, stereopair in occlusal view. **A''**, interpretative drawing of occlusal view; dashed lines represent hypothetical outline restorations. **B**, labial view. **C**, *Chadronycteris rabenae*, SDSM 9931, holotype left maxilla with P4-M3 (reversed for comparison).

Measurement	Quinetia frigidaria	Quinetia misonnei	Stehlinia bonisi	Chadronycteris rabenae	Myotis belgicus
P4-M3 length	5.4	---	---	5.4	---
M1-M3 length	4.3	---	---	4	---
P4 length	1.22	---	1.24-1.31(n=2)	1.45	1.1
P4 width	1.4	---	1.53-1.76 (n=2)	1.6	1.2
M1 length	1.75	1.1	1.64-1.70 (n=2)	1.65	1.60-1.70 (n=2)
M1 width	2.15	1.6	2.00-2.12 (n=2)	2.27	2.10-2.30 (n=2)
M2 length	1.6	1.1-1.3 (n=4)	1.62-1.75 (n=5)	1.8	1.5 (n=3)
M2 width	2.5	1.5 (n=4)	2.27-2.49 (n=7)	2.55	2 (n=3)
M3 length	1.35	---	1.17-1.31 (n=4)	1	0.9
M3 width	2.12	---	1.98-2.14 (n=4)	2.27	1.9

Table 1. Measurements (mm) of *Quinetia frigidaria* sp. nov. (NDGS 1691) from Fitterer Ranch, North Dakota, compared with other Paleogene bats, *Quinetia misonnei* and *Myotis belgicus* (from Gunnell *et al.*, 2017), *Chadronycteris rabenae* (SDSM 9931), *Stehlinia bonisi* (a medium-sized species of the genus; taken from Sigé & Menu, 1995). Sample size is provided when more than 1 specimen was available.

shelf on P4, and having M1 and M2 with postprotocrista not continuous with the metacingulum, thinner lingual cingulum, and distinct paraconule and paraconular crests.

Type locality: Fitterer Ranch locality, Stark County, North Dakota, United States of America.

Horizon and Age: White River Group, Brule Formation, unit 6A of Skinner (1951), early Oligocene, Whitneyan (Korth *et al.*, 2019), ca. 32.0-30.0 Myr (Prothero & Emry, 2004).

Etymology: Latin, frigidaria, "of cooling," referring to the species' occurrence during the time of the transition from Eocene warm conditions to early Oligocene global cooling, a potential incentive driving seasonal torpor in temperate zone bats.

Measurements: See Table 1.

Description:

Quinetia frigidaria is a medium-sized vespertilionid. The M1 and M2 lengths of the holotype NDGS 1691 provide estimates of its body weight ranging from 11.2 g (using M2 length) to 13.6 g (using M1 length) (by method of Czaplewski & Gordon, 2005). This is near the median weight of about 905 species of extant bats (Giannini *et al.*, 2012). In NDGS 1691 the ectolophs of M1 and M2 are damaged labially and the P4 shows slight damage to the cingulum anterolabially and posteriorly. NDGS 1691 preserves part of the palate adjacent to the upper molars (but not reaching the midline of the cranium) and the infraorbital foramen and canal. The infraorbital foramen opens anteriorly dorsal to the posterolabial root of P4; the opening is ovoid in anterior view (Fig. 2B). The infraorbital canal is very short, about as long as the diameter of the infraorbital foramen. At its anterior base the zygomatic arch is 1.2 mm deep and there is a shallow concavity in it above M2. The lower edge of the zygomatic arch curves outward from the tooth row from a point above the distal portion of the M2 ectoloph in occlusal view. Posteriorly, the posterior root of M3 perforates the bone in the floor of the orbit, but the other M3 roots do not. On the palate several small foramina perforate the bone medial to the M2 and M3. The maxillary bone is broken at the mesial edge of P4.

The P4 (Fig. 2A) is dominated by the paracone, which has a slightly curved paracrista that slopes steeply to the metastyle. The metastyle is small but cusplike and is interlocked tightly against the M1 between the M1 parastyle and labial end of the paracingulum, as is typical in vespertilionids. The P4 has a narrow labial cingulum that is interrupted adjacent to the metastyle and forms a short, rounded anterior shelf (on which the enamel is slightly damaged labially) mesial to the paracone. The cingulum is wider anteriorly and continuous with a rounded and well-developed lingual shelf that is rather deeply basined posterior to the paracone, possibly by wear. The lingual cingulum seems to have been continuous around the

lingual shelf and basin to stop at a point just before reaching the metastyle; however, the enamel along this posterior cingulum is damaged, making the basin appear to be open posteriorly. The lingual shelf is not greatly distended posteriorly.

The M1 is broken along the labial edge from the postparacrista to the metastylar area such that the mesostyle and metastyle are missing (Fig. 2A), but the molar was certainly dilambdodont. The tooth is wider than long, with no hint of a hypoconal shelf or hypocone, although the lingual portion of the tooth is slightly distended posteriorly. The tooth bears a large hooked parastyle and strongly W-shaped ectoloph. The lingual cingulum is complete lingually but disappears mesially at the level of the lingual base of the paracone; distally the lingual cingulum is continuous with the postcingulum and reaches the metastyle. There is a relatively deep narrow anterior ectoflexus. Both the parafossa and metafossa are narrow and the parafossa is deeper than the metafossa. The protofossa is deep. The preprotocrista extends anteriorly and labially as a precingulum almost to the parastyle; there is a slight interruption at its labial terminus, with a small notch between the terminus and the parastyle to accommodate the metastyle of the P4. The preprotocrista bears a small paraconule with relatively sharp crests. The postprotocrista bears a small metaconule with a sharp crest (metaloph) on the side facing the protofossa, closing off the protofossa distally, but its distal crest is abbreviated and does not extend beyond the base of the metacone. The paraconule is low and weak but the preparaconule and postparaconule (paraloph) crests are relatively strong. The metaconule is low and weak; the premetaconule crest (metaloph) and postmetaconule crest are relatively strong, but the postmetaconule crest (alternatively interpreted as the distal part of the postprotocrista) is abruptly terminated just distal to the metaconule on M1. The M2 is similar in most aspects to the M1 except for being proportionally wider labiolingually, having the lingual portion of the tooth posterior to the protocone even less distended posteriorly than in the M1, and retaining the premetaconule crest rising up the base of the metacone, but lacking the abbreviated postmetaconule crest of the M1. The ectoloph is broken such that the parastyle and mesostyle are lost. The posterior ectoflexus is relatively deep and narrow, and bears a short ectocingulum. The parastyle is broken but a remnant shows it was hook-like (Fig. 2A"). The postmetacrista is slightly curved and the metastyle forms an unremarkable terminus that probably extended labially beyond the parastyle and mesostyle, and which abuts the parastyle of M3 to form a functionally continuous crest. The lingual cingulum is complete lingually but disappears mesially at the level of the lingual base of the paracone; distally the lingual cingulum is continuous with the postcingulum and reaches the metastyle.

The M3 is reduced, with a smaller protoconal area than those of M1 and M2, and with a metacone about half the height of the paracone (Fig. 2A). The lingual portion of M3 is relatively narrow mesiodistally relative to the ectoloph portion of the

tooth. The ectoloph has a strongly hooked parastyle and lacks a postmetacrista. The centrocrista reaches the labial border of the tooth such that the mesostyle is situated at the labial edge, but the whole edge is shifted lingually, making the postparacrista and premetacrista shorter than the preparacrista and consequently shortening the protofossa. The postparacrista and premetacrista are equal in length. The lingual cingulum nearly disappears at the lingual base of the protocone; mesially it terminates at the level of the lingual base of the paracone, whereas distally it terminates at the level of the lingual base of the metacone. The preprotocrista, paraconule, and precingulum are as in the M1 and M2 (the precingulum is slightly damaged anteriorly). The postprotocrista lacks a metaconule and metaconule crests, and is separated from the lingual base of the metacone by a small notch. From this notch a sharp crest (metaloph?) rises up the lingual face of the metacone. The anterior ectoflexus is deep, and the ectocingulum is rudimentary or absent.

Comparisons:

Comparisons with Quinetia misonnei

As noted by Horácek (2001), there are extensive dental similarities among some North American and European Paleogene and early Miocene vespertilionid fossils. These fossils show a bewildering combination of primitive and derived morphological features (Gunnell *et al.*, 2012). Below we make comparisons with nearly contemporary bats (late Eocene and early Oligocene) from North America and morphologically similar bats from other continents for which the upper teeth are known.

The diagnosis of the genus *Quinetia* is based on data for the lower jaw and teeth only, from the type locality of Hoogbutsel, Belgium, MP21 (Horácek, 2001). However, we refer NDGS 1691 to the genus because new information on the upper teeth was provided by Gunnell *et al.* (2017) based upon isolated specimens associated with lower jaws and teeth from another locality, Boutersem, Belgium, for the only named species *Quinetia misonnei* (Quinet, 1965), which was originally described as a species of *Myotis*. Boutersem and the type locality of Hoogbutsel, Belgium, both date to the early Oligocene, Rupelian (Gunnell *et al.*, 2017), approximately contemporaneous with *Q. frigidaria*. Horácek (2001) erected the new genus *Quinetia* for the taxon *misonnei*. Gunnell *et al.* (2017: fig. 4, pp. 10, 12) described and illustrated two upper molars attributed to *Q. misonnei*, a right M1 and a left M2. These upper molars provide the nearest match for those of *Q. frigidaria*. Although we were unable to examine the Boutersem material of *Q. misonnei*, the figures and description provided by Gunnell *et al.* (2017) made clear the similarity in fine details of dental morphology between the European and North American specimens. Specifically, the upper molars of *Q. frigidaria* resemble those of *Q. misonnei* in being noticeably wider than long, in having two deep ectoflexi, distinct paralophs and metalophs, M2 with metastylar region that extends labially beyond the parastyles and mesostyles, hooklike parastyles, and moderate lingual cingula with no development of a hypocone or hypoconal shelf (cf. Gunnell *et al*., 2017: fig. 4, pp. 10, 12). *Quinetia frigidaria* upper molars differ from the uppers of *Q. misonnei* in size (Table 1), and in having distinct paraconules and the lingual cingulum distally continuous with the postcingulum. Gunnell *et al.* (2017) indicated that the M1 parastyle of *Q. misonnei* is weakly hooked, while their image indicates it is broken but the base of the parastyle shows it was hook-like; they also indicated that the M2 metastyle is distinctly hook-like, but the image shows it to be gently curved with a slight ectocingulum.

We follow Horácek (2001) and Gunnell *et al.* (2017), who placed *Quinetia* in the tribe Plecotini, noting its resemblance especially to *Plecotus*. Gunnell *et al.* (2017) viewed some characters of the upper molars of *Q. misonnei* as relatively primitive compared to extant plecotines, such as having weak metalophs which are absent in extant plecotines leaving the trigon basin open posteriorly. However, the trigon basin in upper molars of some recent plecotines (e.g., *Corynorhinus* and *Barbastella*) are closed posteriorly. Weak metalophs are also present in *Q. frigidaria*. Both *Q. misonnei* and *Q. frigidaria* have trigon basins of M1 and M2 closed posteriorly by the metalophs.

Comparisons with Stehlinia bonisi

Quinetia frigidaria is quite similar in its dentition to European members of *Stehlinia* (?Palaeochiropterygidae or Vespertilionoidea; Smith *et al.*, 2012; Hand *et al.*, 2016), known from the Paleogene (middle Eocene to late Oligocene) of Europe by at least nine species (Eiting & Gunnell, 2009; Smith *et al.*, 2012; Maitre, 2014). Occasional isolated fossils from North America also have been referred to the genus (Ostrander, 1987). *Quinetia frigidaria* shares with *Stehlinia* species, based on descriptions and illustrations from the literature (only original specimens of *Stehlinia bonisi* Sigé, 1990 were available to us for comparison), a suite of relatively primitive characters including upper molars with the same proportions in the ectoloph crests, same labial projection of the mesostyle (preserved in M3, evident although broken in M1 and M2), and moderate degree of reduction of M3 (Sigé & Menu, 1995). In particular it shares with *Stehlinia bonisi* of the late early Oligocene (biochronological level MP 21) of France the same transversely slightly oblong proportions of the P4, slightly "waisted" P4, upper molar lingual flanks slightly depressed along the postprotocrista at the metaconule, fine lophs issuing from the lingual bases of the paracone and metacone directed respectively to the protocone and to the postprotocrista in front of the metaconule, as described for *S. bonisi* and a small indeterminate species from Le Garouillas, France (Sigé & Menu, 1995). *Q. frigidaria* shares with *Stehlinia* the several small foramina in the palate adjacent to the upper molars. It differs from *S. bonisi* in having M1 and M2 with a more reduced angle in the distolingual tooth margin (manifest as a remnant talon or hypoconal shelf, giving a more projecting, angular posterolingual border to the trigon in European *Stehlinia*). The specimen NDGS 1691 has a smaller and less cusplike metaconule on M1 and M2 than *Stehlinia* species. NDGS 1691 has the anterior root of the zygomatic arch arising dorsal to the posterior of M2 instead of above the M3 (as illustrated for *Stehlinia* by Sigé & Menu, 1995: plate 1 fig. 6).

Quinetia frigidaria differs from European *Stehlinia* in having a much shorter infraorbital canal, about as long as the infraorbital foramen is wide, whereas in *Stehlinia* the canal is two to three times as long as the diameter of the infraorbital foramen (based on comparison with *S. bonisi*, and with Sigé, 1974: fig. 1 of *Stehlinia minor*). In *Q. frigidaria* the infraorbital foramen opens dorsal to P4, whereas in *Stehlinia* species whose crania are known (Sigé, 1974: fig. 1), it opens above P3. In *Q. frigidaria* P4 lacks the mid-labial vertical crest that reaches the labial cingulum anterior to the metastyle (Fig. 2), in contrast to *Stehlinia bonisi* P4s, but otherwise no salient

features of P4 seem to distinguish the two taxa. The upper molars of both *Q. frigidaria* and *S. bonisi* lack hypocones, but in *Q. frigidaria* there is no expansion (hypoconal shelf) of the posterolingual portion of the upper molars; in contrast, M1 (but not M2) of *Stehlinia minor* and *S. bonisi* bears a small posterolingual expansion (talon) that creates an indentation of the lingual edge and a median depression of the lingual side of the protocone (Sigé, 1974: fig. 1). In *Q. frigidaria* M1 and M2 show a low paraconule and a metaloph connected to the postprotocrista, while in *S. bonisi* the paraloph tends to join the preprotocrista without forming a paraconule there, and the metaloph attenuates before joining the postprotocrista, leaving the protofossa partially open posteriorly. The M3 in *Q. frigidaria* has a weak paraconule and better-developed paraloph than the M3 of *S. bonisi*, in which the paraconule is absent and the paraloph does not always join the preprotocrista (Sigé, 1974). In *Q. frigidaria* M1-M3 the lingual cingulum is continuous, but in *Stehlinia bonisi* it is interrupted at the lingual base of the protocone in each molar.

Comparisons with Chadronycteris rabenae

Quinetia frigidaria is almost identical in size and quite similar in many details of tooth shapes to *Chadronycteris rabenae* (family uncertain; Gunnell & Simmons, 2005; Smith *et al.*, 2012) of the late Eocene, Chadronian, about 35 Myr, of Nebraska (Ostrander, 1983, 1987; Fig. 2C), while *Q. frigidaria* occurred at about 32 Myr. The holotype of *Q. frigidaria* NDGS 1691 and only known specimen is from the opposite side of the cranium and shows slightly less tooth wear than the holotype of *C. rabenae* SDSM 9931 and only known specimen. Comparative measurements of *Q. frigidaria* and *C. rabenae* are quite similar (Table 1), with a predicted body weight for *Q. frigidaria* of 11.2-13.6 g, and for *C. rabenae* of 11.7-15.3 g. In the preserved portion of the maxillary bone, *Q. frigidaria* differs from *C. rabenae* in having a very short infraorbital canal, whereas in the latter the canal is long and opens a little anterior to P4. The main morphological differences between the two are manifest in details of the teeth. The anterior projection and shelf of P4 of *Q. frigidaria*, slightly damaged on the anterolabial cingulum, protrudes mesially much less than in *C. rabenae*, making the notch between the margins of the anterior shelf and lingual shelf also appear less deep. The lingual shelf of P4 in *Q. frigidaria* is basined, whereas that of *C. rabenae* is barely so, but the difference might be due to different wear in NDGS 1691. The upper molars of *Q. frigidaria* are slightly less inflated or robust than those of *C. rabenae*, and the lingual portion of M3 is slightly narrowed mesiodistally ("waisted") while the lingual portion of M3 in *C. rabenae* is not. In *Q. frigidaria* the M1-M3 have low paraconules and distinct paraconule crests, while these structures are absent in *C. rabenae* (Fig. 2). In *Q. frigidaria* upper molars the postprotocrista is not continuous with the metacingulum (postcingulum), but the lingual cingulum is continuous with the metacingulum, whereas in *C. rabenae* the postprotocrista and metacingulum are continuous (although in the M1 [but not M2] of *C. rabenae* there is a small deviation at the metaconule), and the lingual cingulum does not reach the metacingulum. In *Q. frigidaria* upper molars the ectoflexi (only the anterior is preserved in the M1, and only the posterior is preserved in the M2) are deeper and narrower than in *C. rabenae*. Finally, the lingual cingula of the upper molars are thinner in *Q. frigidaria* than those in *C. rabenae* (Fig. 2).

Among the Vespertilionidae, the earliest known fossils assigned to the family are *Premonycteris vesper* Hand, Sigé, Archer & Black, 2016 from France (Hand *et al.*, 2016) and *Khonsunycteris aegypticus* Gunnell, Simons & Seiffert, 2008 from Egypt (Gunnell *et al.*, 2008), which unfortunately cannot be compared with NDGS 1691 because the only known specimens are dentaries with lower teeth. *Premonycteris vesper* is from the early Eocene, late Ypresian, MP10, about 50 Myr, *Khonsunycteris aegypticus* is from the latest Eocene, Priabonian, about 34 Myr (Gunnell *et al.*, 2008, 2012), while NDGS 1691 occurred about 32 Myr. The European genus *Stehlinia* discussed above, with several species ranging from the middle Eocene to the late Oligocene (about 43-25 Myr), has often been considered as a vespertilionid but more recently has been placed in the extinct European Eocene Palaeochiropterygidae (Gunnell *et al.*, 2012; Maitre, 2014).

By comparison with the oldest known and equivalent-aged *Myotis* species, *M. belgicus* Gunnell, Smith and Smith, 2017 from Europe at about 33 Myr, as characterized by Gunnell *et al.* (2017), *Q. frigidaria* differs in having paraconules and metalophs on M1 and M2, protofossa (trigon basin) of M1 and M2 closed posteriorly, lingual cingulum of M1 and M2 interrupted at base of protocone, M1 and M2 with less developed posterolingual swelling as a remnant of the hypoconal shelf, and M3 relatively long (Table 1).

The only bats yet described from the early Oligocene, Whitneyan are from the late Whitneyan I-75 local fauna, Florida. The I-75 LF bats so far described pertain to the families Emballonuridae, Speonycteridae. Mormoopidae, Natalidae, and Vespertilionidae (Morgan & Czaplewski, personal observervation, 2003; Czaplewski & Morgan, 2012; Morgan *et al.,* 2019). Most of these families differ greatly from *Q. frigidaria*. The sole specimen of a natalid from the I-75 LF is a proximal radius fragment (Morgan & Czaplewski, 2003) that cannot be compared with NDGS 1691 or other North Dakota specimens described herein. The early Miocene (Hemingfordian) natalid *Primonatalus prattae* Morgan & Czaplewski, 2003 of the Thomas Farm local fauna, Florida (Morgan & Czaplewski, 2003), has several differences from *Q. frigidaria*. Unlike *P. prattae, Q. frigidaria* bears a P4 with a much less prominent anterior shelf and adjacent notch and it lacks a labial cingular cusp, its upper molars are transversely wider than long rather than about as wide as they are long, and its M3 lacks a long-crested mesostyle and metaconule. The vespertilionids in the I-75 LF, which might be similar to *Q. frigidaria*, are few in number but have not yet been studied in detail (G. S. Morgan and N. J. Czaplewski, personal observation).

Vespertilionoidea Weber, 1928
Family, genus, and species indeterminate

Referred material: USNM PAL 720182, talonid of a left lower molar; USNM PAL 720179, proximal portion of left humerus; USNM PAL 720180, distal fragment of right humerus lacking the medial epicondyle; USNM PAL 720181, distal portion of left femur.

Description
Among the chiropteran material from North Dakota there is an isolated lower molar talonid, USNM PAL 720182 (not illustrated), on which the transverse width of talonid measures 1.1 mm. The entoconid is broken off; the tooth bears a strong labial cingulum, acute hypoconid, myotodont postcristid, and strong, lingually situated hypoconulid. The fragment is

of a size congruent with the upper molars of *Q. frigidaria*; however, *Quinetia* is characterized by distinctly nyctalodont lower molars (Horácek, 2001) and thus the Fitterer Ranch talonid cannot belong to that genus. It resembles the talonids of *Myotis* as characterized by Gunnell *et al.* (2017) and other vespertilionoid bats. The fragment provides evidence for a second species of bat in the Fitterer Ranch local fauna.

Available equations for using the humerus to estimate bat body mass (Gunnell *et al.*, 2009; Giannini *et al.*, 2012) involve only the midshaft diameter, which is unfortunately unknown in the humerus fragments from Fitterer Ranch. Nevertheless, the Fitterer Ranch humerus and femur fragments compare closely in size with those of the extant North American big brown bat, *Eptesicus fuscus*, a heavier species weighing 14-21 g (Harvey *et al.*, 2011).

The humerus and femur fragments all are slightly abraded or water-worn, although this surface condition might also be the result of their having been prepared in dilute acid (Fig. 3). The postcranials were not directly associated with the maxilla of *Q. frigidaria*, and the proximal humerus fragment USNM PAL 720179 differs in details from a humerus referred to *Quinetia misonnei* by Gunnell *et al.* (2017). The other postcranials lack diagnostic features that would allow them to be matched with *Quinetia*. For this reason, the bat postcranial bones from Fitterer Ranch cannot confidently be referred to *Q. frigidaria*, and probably represent a different species of bat in the fauna.

The proximal humerus fragment USNM PAL 720179 shows a hemispheroidal head with its long axis canted toward the lesser tuberosity, a moderately deep supraglenoid fossa, an elevated pectoral ridge, and a greater tuberosity that extends proximally slightly beyond the head (Fig. 3A-E), which possibly contacted the scapula. The distal fragment USNM PAL 720180 (Fig. 3F-H) does not preserve the entire distal articular surface, but retains the capitulum (medial ridge) and capitular tail (lateral ridge), the latter of which is of reduced diameter and bears a distinct but small proximally directed projection on its rim. Adjacent to this small projection is a well-developed supraepicondylar groove and a deep pit in the lateral end of the lateral epicondyle. The medial ridge of the capitulum is broadly rounded and separated from the capitular tail by a shallow groove. The medial (ventral) half and posterior of the distal humerus fragment are damaged and abraded.

The left femur fragment USNM PAL 720181 (Fig. 3I-L) has slender morphology with reduced distal condyles and a shallow patellar groove as in many other bats. The distal articular end including the condyles in posterior (popliteal) view is about as wide as long. The condyles themselves are moderately elongated, intermediate in proximo-distal diameter, with the lateral condyle broader than the medial condyle, and each is proximodistally longer than wide. In lateral view, the condyles have a somewhat flattened rather than rounded articular surface (Fig. 3K). The intercondylar fossa on the popliteal surface is narrow. Ligamentous attachment areas on the epicondyles and articular surfaces as preserved provide no information on whether or not a tibial lunula, parafibula, or sesamoids other than the femoral patella (Amador *et al.*, 2018) might have been associated with the knee.

Comparisons of postcranials

The Fitterer Ranch humerus fragments morphologically resemble humeri of other vespertilionoids, especially vespertilionids. The Fitterer Ranch proximal humerus shows similar morphology to that of *Stehlinia* (with a "double

scapulo-humeral articulation" [Sigé, 1974], trochiter extending proximally beyond humeral head but lesser trochanter of same height as humeral head, long axis of humeral head canted toward trochiter), but differs in the distal humerus (as far as known in the fragment from Fitterer Ranch) in that the Fitterer Ranch specimen has the articular surfaces apparently aligned with the shaft (judging from the shaft remnant on the fragment; Fig. 3F, G), rather than offset as in *Stehlinia*. The proximal humerus is quite similar to that of many vespertilionid genera extant and extinct. It differs from the humerus attributed to *Q. misonnei* by Gunnell *et al.* (2017), with a shorter trochiter and trochin. The distal humerus differs from molossids and miniopterids in its rounder head, rounded rather than keel-like, angled capitulum, and from *Stehlinia* and natalids in having the distal articular surfaces not offset from the humeral shaft (Sigé, 1974).

The only known early Oligocene bat from North America is the Orellan *Oligomyotis casementi* (Galbreath, 1962). No direct comparison can be made with *O. casementi* because the holotype and only known specimen, a distal humerus, is lost (Czaplewski *et al.*, 2008). In the few anatomical details available in the distal humerus fragment from Fitterer Ranch, the North Dakota fossil resembles Galbreath's (1962: p. 450) word description of *Oligomyotis* in which "the rounded part of the capitulum…is not distinctly keeled as is the case in *Suaptenos* and *Miomyotis*" and "the lateral 'ridge' of the capitulum is much smaller than the main part of the capitulum." However, the Fitterer Ranch specimen has a strongly flaring capitular tail, whereas in *O. casementi* the lateral ridge of the
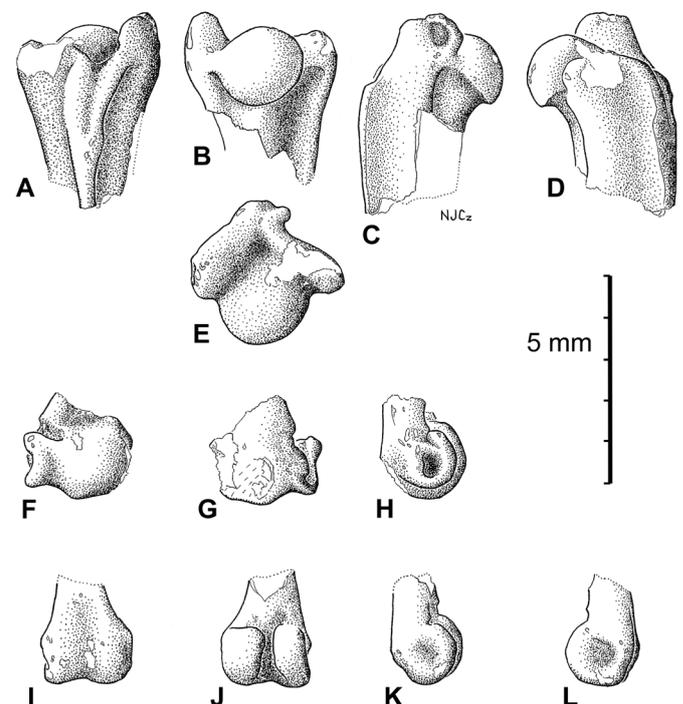
Figure 3. Postcranial bones of early Oligocene bats from Fitterer Ranch, North Dakota. **A-E**, proximal left humerus fragment, USNM PAL 720179, in anterior (A), posterior (B), lateral (dorsal) (C), medial (ventral) (D), and proximal (E) views. **F-H**, distal right humerus fragment, USNM PAL 720180, in anterior (F), posterior (G), and lateral (dorsal) (H) views. **I-L**, distal left femur fragment, USNM PAL 720181, in anterior (I), posterior (J), fibular (K), and tibial (L) views.

capitulum is "without any flare at the margin" (Galbreath, 1962: p. 450). Compared to Galbreath's (1962: fig. 1) illustration, the Fitterer Ranch distal humerus has an apparently more rounded capitulum, and a small, proximally-directed projection on the rim of the capitular tail that is absent in *O. casementi*. In these same characters the North Dakota specimen shows some similarities to two late Oligocene ?vespertilionid humerus fragments from Nebraska (Czaplewski *et al.*, 1999), but all three specimens are too poorly preserved for comparison. In the Fitterer Ranch distal humerus fragment, the medial ridge of the capitulum is more broadly rounded than in the North American Miocene vespertilionids *Suaptenos*, *Miomyotis*, *Karstala* (Lawrence, 1943; Czaplewski & Morgan, 2000) and extant genera with which they were compared such as *Corynorhinus, Myotis, Lasionycteris, Eptesicus*, *Perimyotis, Parastrellus,* and *Lasiurus.*

In the Fitterer Ranch distal femur USNM PAL 720181, the femoral condyles and intercondylar fossa resemble those of extant vespertilionids, miniopterids, and thyropterids (Louzada *et al.*, 2019) in having a narrow intercondylar fossa and elongated rather than broad or rounded condyles. The condyles are relatively shorter proximodistally than in specimens of extant vespertilionids such as *Corynorhinus*, *Myotis, Eptesicus, Lasiurus,* and *Antrozous*, but relatively longer than in *Miniopterus*, molossids, and *Natalus* with which they were compared. Using the characters of the distal femur that were identified by Louzada *et al.* (2019) as being useful in distinguishing modern families of yangochiropteran bats, we find that USNM PAL 720181 most closely resembles the distal femur of vespertilionids and miniopterids in having elongated and somewhat flattened distal condyles. The intercondylar fossa is narrower than in molossids and natalids (as well as other yangochiropteran families as characterized by Louzada *et al.*, 2019), most closely resembling that in vespertilionids and miniopterids. It is possible that the femur fragment pertains to the new North American vespertilionid *Q. frigidaria*, but in light of its early Oligocene age, the incompleteness of the element and its few diagnostic characters, the paucity of other Oligocene bat femurs, and the differences between the Fitterer Ranch fossil humerus fragments and those of the European species *Q. misonnei*, we hesitate to assign any of the postcranials to *Q. frigidaria*. Moreover, because of the similarity of and differences in the distal femur compared to both vespertilionids and miniopterids, we leave the identification of the postcranials in open taxonomy as vespertilionoids until more and better specimens might come to light.

DISCUSSION

The Fitterer Ranch specimens provide the first definitive record of Paleogene bats from North Dakota, and a geographic range extension for the genus *Quinetia* from Europe to North America. We only tentatively place *Q. frigidaria* in the genus *Quinetia* Horácek, 2001 because that genus is diagnosed on the basis of lower tooth characters that are yet unavailable in NDGS 1691. Our assignation depends on Gunnell *et al.*'s (2017) description of isolated upper molars associated with topotype dentaries of *Q. misonnei*, and the similarity of NDGS 1691 to those molars. Following Horácek (2001) and Gunnell *et al.* (2017), we place *Q. frigidaria* in the tribe Plecotini because of many characters of the upper molars shared with extant plecotines, such as protofossae broad and deep, and all cusps and crests slender and sharp. As noted above, both Horácek (2001) and Gunnell

et al. (2017) noted that the upper molars of the Oligocene *Q. misonnei* retained certain relatively primitive features compared to extant plecotines, a paraconule-paraloph, and a metaloph that closes the trigon basin posteriorly. In addition, we note that the North American *Q. frigidaria* exhibits a dental difference in P4 from extant plecotines (P4 is unknown in *Q. misonnei*). Unlike *Q. frigidaria*, the modern taxa *Corynorhinus, Euderma,* and some species of *Plecotus* share presence of an anterolingual cingular cusp in P4, although the cusp is weak or absent in *Barbastella, Idionycteris,* and other *Plecotus* species. It would be desirable to compare *Q. frigidaria* with the earlier-described humerus of *Oligomyotis casementi* from the Orellan of Colorado, but more complete specimens of both taxa and a replacement for the lost holotype and only known specimen of *O. casementi* are needed in order to make any comparisons between them.

Bats underwent a dramatic global radiation in the Eocene, during which ten extinct families and at least the ancestors of the twenty-one extant families appeared (Simmons *et al.*, 2016). One analysis suggests a two-part radiation, with an initial radiation of archaic bats until the Early Eocene Climatic Optimum, followed by a lull from about 49-35 Myr, and another increased diversification rate between about 35 and 25 Myr, initiated in association with the Early Oligocene Glacial Maximum (Yu *et al.*, 2014). The extinct archaic bat family Palaeochiropterygidae, primarily of the middle Eocene of Europe, has been considered ancestral to vespertilionoids or a member of the Vespertilionoidea (Gunnell *et al.*, 2012; Smith *et al.*, 2012). Palaeochiropterygidae contains the early Eocene genera *Palaeochiropteryx, Microchiropteryx, Cecilionycteris*, and *Matthesia* (Smith *et al.*, 2012). The vespertilionid *Quinetia frigidaria* amplifies the late Eocene-early Oligocene radiation of vespertilionids that began as early as the early Eocene with *Premonycteris vesper* of Europe (Hand et al., 2016) and in the early Oligocene includes at least *Khonsunycteris aegyptiacus* of Africa, *Quinetia misonnei, Hanakia fejfari,* and *Myotis belgicus* of Europe (Hand *et al.*, 2016; Gunnell *et al.*, 2017) and *Oligomyotis casementi* of North America (Galbreath, 1962). Indeterminate vespertilionoid and vespertilionid fossils of early Oligocene age hint at additional bat diversity in Kazakhstan (Gabunia & Gabunia, 1987), Yunnan, China (Rich *et al.*, 1983), and Montana, USA (Tabrum *et al.*, 1996).

The earliest fossils recognizable as bats appear in the fossil record about 54 Myr, although molecular studies suggest bats arose earlier, in the Paleocene or late Cretaceous (Teeling *et al.*, 2005; Lei & Dong, 2016). The global climate at this time was decidedly warm, humid, tropical from tropical latitudes well into the polar latitudes (not just in the present-day tropics) (Cramwinckel *et al.*, 2018). The ancestors of bats are predicted to have been tropical in distribution, insectivorous in dietary habits, and scansorial in locomotory ability, with low basal metabolic rates, with early bats developing other dietary, physiological, reproductive, and other specializations after flight (McNab, 1982; Simmons et al., 2008). They probably developed the use of hibernation in response to seasonality in temperatures and availability of food (McNab, 1982) as global climates cooled and temperate and arctic zones developed during the Paleogene. Simmons *et al.* (2016) recently showed that certain archaic bats were probably omnivorous, not strictly insectivorous or arthropodophagous. A few million years after the earliest known fossils of bats are recorded, the global climate underwent a pronounced cooling and Antarctic glaciation during the transition from the end of the Eocene to the early Oligocene (Liu *et al.*, 2009; Goldner *et al.*, 2014). This

transition is interpreted as a drop in mean annual temperature of 8.2 ± 3.1 °C as preserved in stable isotopes in the teeth of mammals in central North America (Zanazzi *et al.*, 2007). The climatic cooling had a profound effect on global vegetation, which in North America transitioned from paleofloras of warm, decidedly tropical character extending to the present-day Arctic Circle during the Eocene to drier, more seasonal, open shrublands occurring in the continental interior in the early Oligocene (Graham, 1999; Collinson, 2000). Thus, tropical conditions in the middle Eocene extended to Ellesmere Island at 81° N latitude (Graham, 1999; the Fitterer Ranch locality is near 46° 45' N latitude). Although no fossil floras of late Eocene to early Oligocene age are known in North Dakota, paleofloras in Montana show a stepwise sequence from moist forest to dry forest to dry deciduous woodland to open wooded habitat with gallery forests (Graham, 1999), and paleosols in the White River Group in South Dakota and surrounding region indicate a humid and subtropical climate that later became subhumid and cool temperate (Retallack, 1983, 2007). Contemporaneous records of ectothermic vertebrates from the region are sparse, but alligators may have adapted to the cooling temperatures or began to disappear from the northern Great Plains in the early Oligocene, as did aquatic turtles (Hutchison, 1992; Corsini *et al.*, 2011; Whiting & Hastings, 2015). The cooling caused the Grande Coupure faunal turnover in Europe (Stehlin, 1909; Woodburne, 2004), while the Antarctic glaciation drew down sea levels and facilitated intercontinental dispersals of terrestrial mammals through Beringia, resulting in similarities between Eocene-Oligocene Asian and North American assemblages (Graham, 1999, Woodburne, 2004). Stucky (1992), Woodburne (2004) and Zanazzi *et al.* (2007) noted relatively minor effects of the cooling on North American mammals (but pronounced effects on heterothermic vertebrates) during the early Oligocene, as evidenced by relatively mild faunal turnover in the Chadronian-Orellan and Orellan-Whitneyan and by stable isotopes in mammal bones from the central Great Plains during the Eocene-Oligocene transition, respectively. However, Yu *et al.* (2014) reported heightened bat diversification rates during the much longer time span 35-25 Myr, and inferred that "intrinsic innovations or adaptations may have released some lineages from the intense selective pressures associated with these severe [global cooling] conditions." *Stehlinia* and other early members of a vespertilionoid radiation probably moved from Asia to North America in the Eocene prior to the early Oligocene cooling via continental connections that had already established a Holarctic corridor by the early Oligocene (McKenna, 1975; Müller *et al.*, 2008).

Quinetia frigidaria reflects the beginnings of the plecotine (and vespertilionid) radiation at a relatively high temperate latitude in North America concomitant with early Oligocene seasonal/climatic, floral, insect faunal, and biogeographic changes. Vespertilionids are the most widespread bat family in the temperate zone (Simmons, 2005) and include the most species undergoing hibernation and seasonal migration. Many extant plecotine bats hibernate, but they migrate only locally (Fleming & Eby, 2003). It is tempting to cite the Eocene-Oligocene climatic transition and global cooling as a potential causative factor in the evolution of aspects of the physiology and behavior of vespertilionids or other bats such as heterothermy and migration. However, current evidence suggests that the most recent common ancestor of crown-group bats might have been capable of daily heterothermy (Lazzeroni *et al.*, 2018). Hibernation appears to have evolved several times independently among extant bats including some tropical and subtropical species, and current views of the thermoregulatory physiology of mammals suggests a continuum of ability from homeothermy to daily torpor to hibernation (Geiser & Stawski, 2011; Lazzeroni *et al.*, 2018). Geiser & Stawski (2011) argued that extended torpor evolved in the tropics and subtropics before bats had invaded temperate climates or were exposed to prolonged cold temperatures. Vespertilionids make up nearly one-third of all extant bats and are the most widespread extant family geographically (Simmons, 2005). Horácek (2001) remarked about the vespertilionid radiation being characterized by "metabolic and behavioural versatility" of these bats with respect to their echolocation style and capability for thermoregulation compared to other bat families characterized by morphological specializations. As primarily insectivorous bats for whom insect availability probably became increasingly more seasonal, vespertilionid bats in particular assumed a more seasonal food and lifestyle, driving the evolution of a seasonal migration or hibernation physiology, and enabling their radiation through the developing late Cenozoic temperate zone.

ACKNOWLEDGMENTS

BIBLIOGRAPHY

Amador, L. I., Giannini, N. P., Simmons, N. B., Abdala, V., 2018. Morphology and evolution of sesamoid elements in bats (Mammalia: Chiroptera). American Museum Novitates 3905, 1-38. https://doi.org/10.1206/3905.1

Black, C. C., 1961. Rodents and lagomorphs from the Miocene Fort Logan and Deep River Formation of Montana. Postilla 48, 1-20.

Blumenbach, J. F., 1779-1780. Handbuch der Naturgeschichte. Johann Christian Dieterich, Göttingen.

Collinson, M. E., 2000. Cenozoic evolution of modern plant communities and vegetation. In: Culver, S. J., Rawson, P. F. (Eds.), Biotic Response to Global Change: The Last 145 Million Years. Cambridge University Press, Cambridge, pp. 223-243. https://doi.org/10.1017/CBO9780511535505.017

Corsini, J. A., Smith, T. R., Leite, M. B., 2011. Turtle decline in the early Oligocene of western Nebraska. Journal of Herpetology 45, 238-243. https://doi.org/10.1670/10-052.1

Cramwinckel, M. J., Huber, M., Kocken, I. J., Agnini, C., Bijl, P. K., Bohaty, S. M., Frieling, J., Goldner, A., Hilgen, F. J., Kip, E. L., Peterse, F., van der Ploeg, R., Röhl, U., Schouten, S., Sluijs, A., 2018. Synchronous tropical and polar temperature evolution in the Eocene. Nature 559, 382-386. https://doi.org/10.1038/s41586-018-0272-2

Crochet, J.-Y., Hartenberger, J. L., Rage, J.-C., Rémy, J. A., Sigé, B., Sudre, J., Vianey-Liaud, M., 1981. Les nouvelles faunes de vertébrés antérieures à la "Grande Coupure" découvertes dans les phosphorites du Quercy. Bulletin Museum National de l'Histoire Naturelles, Paris 3, 245-265.

Czaplewski, N. J., Gordon, C. L., 2005. Relationship of body weight

and molar size in bats and the prediction of body mass in some extinct species. Journal of Vertebrate Paleontology 25(3, supplement: Abstracts of Papers), 48A.

Czaplewski, N. J., Morgan, G. S., 2012. New basal noctilionoid bats (Mammalia: Chiroptera) from the Oligocene of subtropical North America. In: Gunnell, G. F., Simmons, N. B. (Eds.), Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge, pp. 162-209. https://doi.org/10.1017/CBO9781139045599.006

Czaplewski, N. J., Bailey, B. E., Corner, R. G., 1999. Tertiary bats (Mammalia: Chiroptera) from northern Nebraska. Transactions of the Nebraska Academy of Sciences 25, 83-93.

Czaplewski, N. J., Morgan, G. S., McLeod, S. A., 2008. Chiroptera. In: Janis, C. M., Gunnell, G. F., Uhen, M. D. (Eds.), Evolution of Tertiary Mammals of North America, vol. 2: Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge, pp. 174-197. https://doi.org/10.1017/CBO9780511541438.013

Czaplewski, N. J., Morgan, G. S., Naeher, T., 2003. Molossid bats from the late Tertiary of Florida with a review of the Tertiary Molossidae of North America. Acta Chiropterologica 5, 61-74. https://doi.org/10.3161/001.005.0105

Eiting, T. P., Gunnell, G. F., 2009. Global completeness of the bat fossil record. Journal of Mammalian Evolution 16, 151-173. https://doi.org/10.1007/s10914-009-9118-x

Emry, R. J., and Korth, W. W., 2007. A new genus of squirrel (Rodentia, Sciuridae) from the mid-Cenozoic of North America. Journal of Vertebrate Paleontology 27, 693-698. https://doi.org/10.1671/0272-4634(2007)27[693:ANGOSR]2.0.CO;2

Fleming, T. H., Eby, P., 2003. Ecology of bat migration. In: Kunz, T. H., Fenton. M. B. (Eds.), Bat Ecology. University of Chicago Press, Chicago, pp. 156-208.

Gabunia, L. K., Gabunia, V. J., 1987. On the first find of fossil bats (Chiroptera) in the Paleogene of the USSR. Bulletin of the Academy of Sciences of the Georgian SSR 126, 197-200.

Galbreath, E. C., 1962. A new myotid bat from the middle Oligocene of northeastern Colorado. Transactions of the Kansas Academy of Science 65, 448-451. https://doi.org/10.2307/3626776

Geiser, F., Stawski, C., 2011. Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. Integrative and Comparative Biology 51, 337-348. https://doi.org/10.1093/icb/icr042

Giannini, N. P., Gunnell, G. F., Habersetzer, J., Simmons, N. B., 2012. Early evolution of body size in bats. In: Gunnell, G. F., Simmons, N. B. (Eds.) Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge, pp. 530-555. https://doi.org/10.1017/CBO9781139045599.017

Goldner, A., Herold, N., Huber, M., 2014. Antarctic glaciation caused ocean circulation changes at the Eocene-Oligocene transition. Nature 511, 574-577; erratum 519, 378. https://doi.org/10.1038/nature13597

Graham, A., 1999. Late Cretaceous and Cenozoic History of North American Vegetation North of Mexico. Oxford University Press, New York.

Gray, J. E., 1821. On the natural arrangement of vertebrose animals. London Medical Repository, Monthly Journal, and Review 15, 296-311.

Gray, J. E., 1866. Synopsis of the genera of the Vespertilionidae and Noctilionidae. Annals and Magazine of Natural History ser. 3, 17, 89-93. https://doi.org/10.1080/00222936608679488

Gunnell, G. F., Simmons, N. B., 2005. Fossil evidence and the origin of bats. Journal of Mammalian Evolution 12, 209-246. https://doi.org/10.1007/s10914-005-6945-2

Gunnell, G. F., Butler, P. M., Greenwood, M., Simmons, N. B., 2015. Bats (Chiroptera) from Olduvai Gorge, early Pleistocene, Bed I (Tanzania). American Museum Novitates 3846, 1-35. https://doi.org/10.1206/3846.1

Gunnell, G. F., Simons, E. L., Seiffert, E. R., 2008. New bats (Mammalia: Chiroptera) from the late Eocene and early Oligocene, Fayum Depression, Egypt. Journal of Vertebrate Paleontology 28, 1-11. https://doi.org/10.1671/0272-4634(2008)28[1:NBMCFT]2.0.CO;2

Gunnell, G. F., Worsham, S. R., Seiffert, E. R., Simons, E. L., 2009. *Vampyravus orientalis* Schlosser (Chiroptera) from the Early Oligocene (Rupelian), Fayum, Egypt—body mass, humeral morphology and affinities. Acta Chiropterologica 11, 271-278. https://doi.org/10.3161/150811009X485512

Gunnell, G. F., Eiting, T. P., Simons, E. L., 2012. African Vespertilionoidea (Chiroptera) and the antiquity of Myotinae. In: Gunnell, G. F., Simmons, N. B. (Eds.) Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge, pp. 252-266. https://doi.org/10.1017/CBO9781139045599.008

Gunnell, G. F., Smith, R., Smith, T., 2017. 33 million year old *Myotis* (Chiroptera, Vespertilionidae) and the rapid global radiation of modern bats. PLoS One 12(3), e0172621. https://doi.org/10.1371/journal.pone.0172621

Hand, S. J., Sigé, B., Archer, M., Black, K. H., 2016. An evening bat (Chiroptera: Vespertilionidae) from the late Early Eocene of France, with comments on the antiquity of modern bats. Palaeovertebrata 30, 227-236. https://doi.org/10.18563/pv.40.2.e2

Harvey, M. J., Altenbach, J. S., Best, T. L., 2011. Bats of the United States and Canada. Johns Hopkins University Press, Baltimore.

Hoganson, J. W., Lammers, G. E., 1985. The vertebrate fauna and paleoecology of the Dickinson member, Brule Formation (Oligocene) in Stark County, North Dakota. Proceedings of the North Dakota Academy of Science 39, 15.

Hoganson, J. W., Lammers, G. E., 1992. Vertebrate fossil record, age and depositional environments of the Brule Formation (Oligocene) in North Dakota. In: Erickson, J. M., Hoganson, J. W. (Eds.), Frank D. Holland, Jr. Symposium. North Dakota Geological Survey Miscellaneous Series 76, 243-257.

Hoganson, J.W., Murphy, E.C., Forsman, N.F., 1998. Lithostratigraphy, paleontology, and biochronology of the Chadron, Brule, and Arikaree Formations in North Dakota. In: Terry, D. O., LaGarry, H. E., Hunt, R. M. (Eds.), Depositional Environments, Lithostratigraphy, and Biostratigraphy of the White River and Arikaree Groups (Late Eocene to Early Miocene, North America). Geological Society of America Special Paper 325, 185-196. https://doi.org/10.1130/0-8137-2325-6.185

Horácek, I., 2001. On the early history of vespertilionid bats in Europe: the lower Miocene record from the Bohemian Massif. Lynx (Praha) 37, 131-150.

Hutchison, J. H., 1992. Western North American reptile and amphibian record across the Eocene/Oligocene boundary and its climatic implications. In: Prothero, D. R., Berggren, W. A. (Eds.), Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, pp. 451-463. https://doi.org/10.1515/9781400862924.451

Janis, C. M., Gunnell, G. F., Uhen, M. D. (Eds.), 2008. Evolution of Tertiary Mammals of North America. Volume 2: Small Mammals, Xenarthrans, and Marine Mammals. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511541438

Kihm, A. J., Lammers, G. E., 1986. Vertebrate biochronology of Oligocene sediments in southwest North Dakota. Proceedings of the North Dakota Academy of Science 40, 18.

Koopman, K. F., 1985. A synopsis of the families of bats – Part VII. Bat Research News 25(3/4), 25-27.

Korth, W. W., 2007. Mammals from the Blue Ash local fauna (late Oligocene), South Dakota. Rodentia, part 1: families Eutypomyidae, Eomyidae, Heliscomyidae, and *Zetamys*. Paludicola 6, 31-40.

Korth, W. W., 2010. Mammals from the Blue Ash Local Fauna (late Oligocene), South Dakota. Rodentia Part 5: Family Cricetidae. Paludicola 7(4), 117-136.

Korth, W. W., 2014. Rodents (Mammalia) from the Whitneyan (middle Oligocene) Cedar Pass Fauna of South Dakota. Annals of Carnegie Museum 82, 373-398. https://doi.

org/10.2992/007.082.0404

Korth, W. W., 2019. Rodents (Mammalia) from the early Oligocene (Orellan) Cook Ranch local fauna of southwestern Montana. Annals of Carnegie Museum 85, 91-111. https://doi.org/10.2992/007.085.0303

Korth, W. W., Emry, R. J., Boyd, C. A., Person, J. J., 2019. Rodents (Mammalia) from Fitterer Ranch, Brule Formation (Oligocene), North Dakota. Smithsonian Contributions to Paleobiology 103, 1-45. https://doi.org/10.5479/si.1943-6688.103

Lawrence, B., 1943. Miocene bat remains from Florida, with notes on the generic characters of the humerus of bats. Journal of Mammalogy 24, 356-369. https://doi.org/10.2307/1374836

Lazzeroni, M. E., Burbrink, F. T., Simmons, N. B., 2018. Hibernation in bats (Mammalia: Chiroptera) did not evolve through positive selection of leptin. Ecology and Evolution 2018, 1-21. https://doi.org/10.1002/ece3.4674

Lei, M., Dong, D., 2016. Phylogenomic analyses of bat subordinal relationships based on transcriptome data. Scientific Reports 6, 27726. https://doi.org/10.1038/srep27726

Leidy, J., 1869. The extinct mammalian fauna of Dakota and Nebraska, including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. Journal of the Academy of Natural Sciences, Philadelphia 2, 1-472. https://doi.org/10.5962/bhl.title.20910

Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymiis, locis. Editio decima, reformata. Laurentii Salvii, Stockholm, vol. 1, 824 pp. https://doi.org/10.5962/bhl.title.542

Liu, Z., Pagani, M., Zinniker, D., DeConto, R., Huber, M., Brinkhuis, H., Shah, S. R., Leckie, R. M., Pearson, A., 2009. Global cooling during the Eocene-Oligocene climate transition. Science 323, 1187-1190. https://doi.org/10.1126/science.1166368

Louzada, N. S. V., Norgueira, M. R., Pessôa. 2019. Comparative morphology and scaling of the femur in yangochiropteran bats. Journal of Anatomy 235, 124-150. https://doi.org/10.1111/joa.12996

Maitre, E., 2014. Western European middle Eocene to early Oligocene Chiroptera: systematics, phylogeny and palaeoecology based on new material from the Quercy (France). Swiss Journal of Palaeontology 133, 141-242. https://doi.org/10.1007/s13358-014-0069-3

McKenna, M. C., 1975. Fossil mammals and early Eocene North Atlantic land continuity. Annals of the Missouri Botanical Garden 62, 335-353. https://doi.org/10.2307/2395200

McNab, B. K., 1982. Evolutionary alternatives in the physiological ecology of bats. In: Kunz, T. H. (Ed.), Ecology of Bats. Plenum Press, New York, pp. 151-200. https://doi.org/10.1007/978-1-4613-3421-7_4

Morgan, G. S., Czaplewski, N. J., 2003. A new bat (Chiroptera: Natalidae) from the Early Miocene of Florida, with comments on natalid phylogeny. Journal of Mammalogy 84, 729-752. https://doi.org/10.1644/1545-1542(2003)084<0729:ANBCNF>2.0.CO;2

Morgan, G. S., Czaplewski, N. J., Simmons, N. B., 2019. A new mormoopid bat from the Oligocene (Whitneyan and early Arikareean) of Florida, and phylogenetic relationships of the major clades of Mormoopidae (Mammalia: Chiroptera). Bulletin of the American Museum of Natural History 434, 1-141. https://doi.org/10.1206/0003-0090.434.1.1

Müller, R. D., Sdrolias, M., Gaina, C., Steinberger, B., Heine, C., 2008. Long-term sea-level fluctuations driven by ocean basin dynamics. Science 319, 1357-1362. https://doi.org/10.1126/science.1151540

Murphy, E. C., Hoganson, J. W., Forsman, N. F., 1993. The Chadron, Brule, and Arikaree Formations in North Dakota. North Dakota Geological Survey Report of Investigations 96, 1-144.

O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T. J., Giallombardo, A., Giannini, N. P., Goldberg, S. L., Kraatz, B. P., Luo, Z.,

Meng, J., Ni, X., Novacek, M. J., Perini, F. A., Randall, Z. S., Rougier, G. W., Sargis, E. J., Silcox, M. T., Simmons, N. B., Spaulding, M., Velazco, P. M., Weksler, M., Wible, J. R., Cirranello, A. L., 2013. The placental mammal ancestor and the post–K-Pg radiation of placentals. Science 339, 662-667. https://doi.org/10.7934/P773

Ostrander, G. E., 1983. New early Oligocene (Chadronian) mammals from the Raben Ranch local fauna, northwest Nebraska. Journal of Paleontology 57, 128-139.

Ostrander, G. E., 1985. Correlation of the early Oligocene (Chadronian) in northwestern Nebraska. Dakoterra 2, 205-231.

Ostrander, G. E., 1987. The early Oligocene (Chadronian) Raben Ranch local fauna, northwest Nebraska: Marsupialia, Insectivora, Dermoptera, Chiroptera, and Primates. Dakoterra 3, 92-104.

Pearson, P. N., van Dongen, B. E., Nicholas, C. J., Pancost, R. D., Schouten, S., Singano, J. M., Wade, B. S., 2007. Stable warm tropical climate through the Eocene epoch. Geology 35, 211-214. https://doi.org/10.1130/G23175A.1

Prothero, D. R., Emry, R. J., 2004. The Chadronian, Orellan, and Whitneyan North American Land Mammal Ages. In: Woodburne, M. O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America Biostratigraphy and Geochronology. Columbia University Press, New York, pp. 156-168. https://doi.org/10.7312/wood13040-007

Quinet, G. E., 1965. Myotis misonnei n. sp. - chiroptère de l'Oligocène de Hoogbutsel. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 41, 1-11.

Ravel, A., Adaci, M., Bensalah, M., Charruault, A.-L., Essid, E. M., Ammar, H. K., Marzougui, W., Mahboubi, M., Mebrouk, F., Merzeraud, G., Vianey-Liaud, M., Tabuce, R., Marivaux, L., 2016. Origine et radiation initials des chauves-souris modernes: nouvelles découvertes dans l'Éocène d'Afrique du Nord. Geodiversitas 38, 355-434.

Retallack, G. J., 1983. Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota. Geological Society of America Special Paper 193, 1-82. https://doi.org/10.1130/SPE193-p1

Retallack, G. J., 2007. Cenozoic paleoclimate on land in North America. Journal of Geology 115, 271-294. https://doi.org/10.1086/512753

Revilliod, P., 1919. L'état actuel de nos connaissances sur les Chiroptères fossiles (Note Préliminaire). Compte rendu des séances de la Société de physique et d'histoire naturelle de Genève 36, 93-96.

Rich, T. H. V., Yu-Ping, Z., Hand, S. J., 1983. Insectivores and a bat from the Early Oligocene Caijiachong Formation of Yunnan, China. Australian Mammalogy 6, 61-75.

Schultz, C. B., and Falkenbach, C. H., 1956. Miniochoerinae and Oreonetinae two new subfamilies of oreodonts. Bulletin of the American Museum of Natural History 109, 373-482.

Sheldon, N.D., Retallack, G. J., 2004. Regional paleoprecipitation records from the Late Eocene and Oligocene of North America. Journal of Geology 112, 487–494. https://doi.org/10.1086/421076

Shi, J. J., Rabosky, D. L., 2015. Speciation dynamics during the global radiation of extant bats. Evolution 69, 1528-1545. https://doi.org/10.1111/evo.12681

Sigé, B., 1974. Données nouvelles sur le genre Stehlinia (Vespertilionoidea, Chiroptera) du Paléogène d'Europe. Palaeovertebrata 6, 253-272.

Sigé, B., 1990. Nouveaux chiroptères de l'Oligocène moyen des Phosphorites du Quercy, France. Compte rendu de l'Académie des Sciences de Paris 310, 1131-1137.

Sigé, B., Legendre, S., 1983. L'histoire des peuplements de chiroptères du bassin Méditerranéen: l'apport compare des remplissages karstiques et des dépôts fluvio-lacustres. Mémoires de Biospéologie 10, 209-225.

Sigé, B., Menu, H., 1995. Le Garouillas et les sites contemporains (Oligocene, MP 25) des phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de vertebres 5. Chiropteres.

Palaeontographica 236, 77-124.

Simmons, N. B., 2005. Order Chiroptera. In: Wilson, D. E., Reeder, D. M. (Eds.), Mammal Species of the World A Taxonomic and Geographic Reference, Third Edition, volume 1. Johns Hopkins University Press, Baltimore, pp. 312-529.

Simmons, N. B., Cirranello, A. L., 2018. Bat species of the world: a taxonomic and geographic database. http://batnames.org. Accessed 4 December 2018.

Simmons, N.B., Seiffert, E. R., Gunnell, G.F., 2016. A new family of large omnivorous bats (Mammalia, Chiroptera) from the late Eocene of the Fayum Depression, Egypt, with comments on use of the name "Eochiroptera." American Museum Novitates 3857, 1-43. https://doi.org/10.1206/3857.1

Simmons, N. B., Seymour, K. L., Habersetzer, J., Gunnell, G. F., 2008. Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451, 818-822. https://doi.org/10.1038/nature06549

Skinner, M. F., 1951. The Oligocene of western North Dakota. In: Bump, J. D. (Ed.), Society of Vertebrate Paleontology Guidebook, 5th Annual Field Conference, Western South Dakota, August-September 1951, pp. 51-58.

Smith, T., Habersetzer, J., Simmons, N. B., Gunnell, G. F., 2012. Systematics and paleobiogeography of early bats. In: Gunnell, G. F., Simmons, N. B. (Eds.), Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge, pp. 23-66. https://doi.org/10.1017/CBO9781139045599.003

Stehlin, H. G., 1909. Remarques sur les faunules de Mammifères des couches éocènes et oligocènes du Bassin de Paris. Bulletin de la Société géologique de France ser. 4 9, 488-520.

Stirton, R. A., 1935. A review of the Tertiary beavers. University of California Publications, Bulletin of the Department of Geological Sciences 23, 391-458.

Stone, W. J., 1973. Stratigraphy and sedimentary history of middle Cenozoic (Oligocene and Miocene) deposits in North Dakota. PhD dissertation, University of North Dakota, Grand Forks, 217 pp.

Storer, J. E., 2002. Small mammals of the Kealey Springs local fauna (early Arikareean; late Oligocene) of Saskatchewan. Paludicola 3, 105-133.

Stucky, R. K., 1992. Mammalian faunas in North America of Bridgerian to early Arikareean "ages" (Eocene and Oligocene). In: Prothero, D. R., Berggren, W. A. (Eds.), Eocene-Oligocene Climatic and Biotic Evolution. Princeton University Press, Princeton, pp. 464-493. https://doi.org/10.1515/9781400862924.464

Swisher, C. C., 1982. Stratigraphy and biostratigraphy of the eastern portion of Wildcat Ridge, western Nebraska. M. S. thesis, University of Nebraska, Lincoln.

Tabrum, A. R., Prothero, D. R., Garcia, D., 1996. Magnetostratigraphy and biostratigraphy of the Eocene-Oligocene transition, southwestern Montana. In: Prothero, D. R., Emry, R. J. (Eds.), The Terrestrial Eocene-Oligocene Transition in North America. Cambridge University Press, Cambridge, pp. 278-311. https://doi.org/10.1017/CBO9780511665431.015

Tedford, R. H., Albright III, B. A., Barnosky, A. D., Ferrusquía-Villafranca, I., Hunt Jr., R. M., Storer, J. E., Swisher III, C. C., Voorhies, M. R., Webb, S. D., Whistler, D. P., 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). In: Woodburne, M. O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America Biostratigraphy and Geochronology. Columbia University Press, New York, pp. 169-231. https://doi.org/10.7312/wood13040-008

Teeling, E. C., Springer, M. S., Madsen, O., Bates, P., O'Brien, S. J., Murphy, W. J., 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307, 580-584. https://doi.org/10.1126/science.1105113

Teeling, E. C., Dool, S., Springer, M. S., 2012. Phylogenies, fossils and functional genes: the evolution of echolocation in bats. In: Gunnell, G. F., Simmons, N. B. (Eds.), Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge, pp. 1-22. https://doi.org/10.1017/CBO9781139045599.002

Vaughan, T. A., 1959. Functional morphology of three bats: *Eumops, Myotis, Macrotus*. University of Kansas Publications Museum of Natural History 12, 1-153.

Weber, M., 1927-1928. Die Säugetiere. Gustav Fischer, Jena, vol. 1, Anatomischer Teil (1927, with collaboration of H. M. de Burlet), xv + 444 pp.; vol. 2, Systematischer Teil (1928, with collaboration of Othenio Abel), xxiv + 898 pp.

Whiting, E. T., Hastings, A. K., 2015. First fossil *Alligator* from the Late Eocene of Nebraska and the late Paleogene record of alligators in the Great Plains. Journal of Herpetology 49, 560-569. https://doi.org/10.1670/14-069

Wood, A. E., 1937. The mammalian fauna of the White River Oligocene: Part II. Rodentia. Transactions of the American Philosophical Society 28, 155-269. https://doi.org/10.2307/1005501

Woodburne, M. O., 2004. Global events and the North American mammalian biochronology. In: Woodburne, M. O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America Biostratigraphy and Geochronology. Columbia University Press, New York, pp. 315-343. https://doi.org/10.7312/wood13040

Yu, W., Wu, Y., Yang, G., 2014. Early diversification trend and Asian origin for extent [sic] bat lineages. Journal of Evolutionary Biology 27, 2204-2218. https://doi.org/10.1111/jeb.12477

Zachos, J. C., Dickens, G. R., Zeebe, R. E., 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature 451, 279-283. https://doi.org/10.1038/nature06588

Zanazzi, A., Kohn, M. J., MacFadden, B. J., Terry Jr., D. O., 2007. Large temperature drop across the Eocene-Oligocene transition in central North America. Nature 445, 639-642. https://doi.org/10.1038/nature05551

Ziegler, R., 2000. The bats (Chiroptera, Mammalia) from the Late Oligocene fissure fillings Herrlingen 8 and Herrlingen 9 near Ulm (Baden-Württemberg). Senckenbergiana Lethaea 80, 647-683. https://doi.org/10.1007/BF03043368