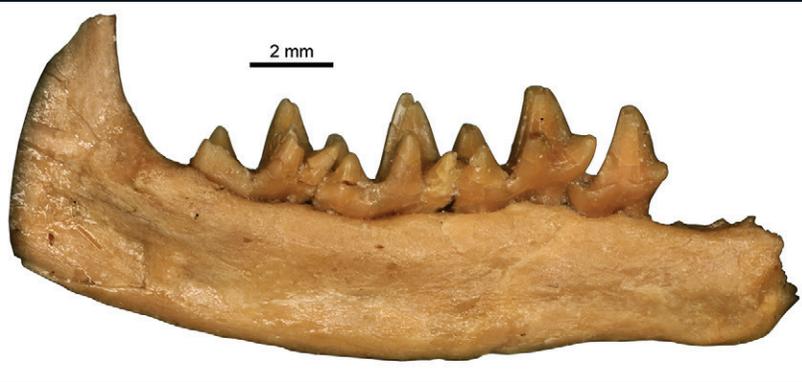




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Three New Early Middle Eocene Bats (Mammalia: Chiroptera) from Elderberry Canyon, Nevada, USA

*Nicholas J. Czaplewski, Gary S. Morgan,
Robert J. Emry, Paul M. Gignac,
and Haley D. O'Brien*

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ABSTRACT

Czaplewski, Nicholas J., Gary S. Morgan, Robert J. Emry, Paul M. Gignac, and Haley D. O'Brien. Three New Early Middle Eocene Bats (Mammalia: Chiroptera) from Elderberry Canyon, Nevada, USA. *Smithsonian Contributions to Paleobiology*, number 106, viii + 26 pages, 11 figures, 3 tables, 2022. — We report three new taxa of bats from the late early Eocene to earliest middle Eocene (Bridgerian biochrons Br1b–Br2; ca. 50–48 Ma) Elderberry Canyon Quarry, Sheep Pass Formation, in the Egan Mountain Range of eastern Nevada, USA. *Volatrix simmonsae* gen. et sp. nov., represented by two dentaries, is tentatively referred to the family ?Onychonycteridae and exhibits a p3 that is much smaller than the p2, a semimolariform p4, and lower molars with a postcristid configuration intermediate between necromantodonty and nyctalodonty. The genus *Palaeochiropteryx*, a palaeochiropterygid otherwise known from the early and middle Eocene of Europe, is the first representative of its genus and of the family Palaeochiropterygidae outside Eurasia and the Indo-Pakistan subcontinent. *Palaeochiropteryx* is represented at the site by a partial skeleton with a crushed skull and two left dentaries (one unexposed within the same limestone block but revealed by micro-computed tomography scanning) and is formally named *Palaeochiropteryx sambuceus* sp. nov. A third taxon, *Sonor handae* gen. et sp. nov., is a probable vespertilionid, evidenced by a dentary fragment with double-rooted p3 and myotodont lower molar morphology, and provides the earliest occurrence of the family Vespertilionidae in the Western Hemisphere. Despite the small number of specimens, these three new taxa comprise the most diverse Eocene assemblage of bats yet found in a single quarry in the Western Hemisphere.

RESUMEN

Czaplewski, Nicholas J., Gary S. Morgan, Robert J. Emry, Paul M. Gignac y Haley D. O'Brien. Three New Early Middle Eocene Bats (Mammalia: Chiroptera) from Elderberry Canyon, Nevada, USA. *Smithsonian Contributions to Paleobiology*, numero 106, viii + 26 paginas, 11 figuras, 3 tablas, 2022. — Reportamos tres nuevos taxones de murciélagos desde finales del Eoceno Temprano hasta el Eoceno Medio el más temprano (NALMA Bridgerian, los biocronos Br1b–Br2; ca. 50–48 Ma) de la Cantera Elderberry Canyon, Formación Sheep Pass, en la Cordillera Egan de este de Nevada, EE.UU. *Volatrix simmonsae* gen. et sp. nov. se refiere tentativamente a la familia ?Onychonycteridae y está representado por dos dentarios que muestran un p3 mucho más pequeña que el p2, un p4 semimolariforme y molares inferiores con una configuración poscrística intermedia entre necromantodontia y nictalodontia. El género *Palaeochiropteryx*, un palaeochiropterygid conocido desde el Eoceno temprano y medio de Europa, es el primer representante de su género y de la familia Palaeochiropterygidae fuera de Eurasia y el subcontinente Indo-Pakistáni. *Palaeochiropteryx* está representado en el sitio por un esqueleto parcial con cráneo aplastado y dos dentaries izquierdos (uno no expuesto dentro del mismo bloque de piedra caliza pero revelado por escaneo microCT) y formalmente se llama *Palaeochiropteryx sambuceus* sp. nov. Un tercer taxón, *Sonor handae* gen. et sp. nov., es un vespertilionid probable, evidenciado por un fragmento de dentario con p3 de doble raíz, y molares inferiores con morfología miotodonte, y proporciona la aparición más temprana de la familia Vespertilionidae en el hemisferio occidental. A pesar del pequeña número de especímenes, estos tres nuevos taxones comprenden el conjunto de murciélagos del Eoceno más diverso que se haya encontrado en una sola cantera en el hemisferio occidental.

Cover images: Left, *Volatrix simmonsae* gen. et sp. nov., USNM PAL 417351, paratype horizontal ramus in lingual view (detail from Figure 2; photo by N. J. Czaplewski). Right, possibly *Palaeochiropteryx sambuceus*, rendered from μ CT scan of left dentary with p4–m3 in labial view (detail from Figure 8; photo by Haley D. O'Brien).

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Three New Early Middle Eocene Bats (Mammalia: Chiroptera) from Elderberry Canyon, Nevada, USA

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Paul M. Gignac,⁴ and Haley D. O'Brien⁴

INTRODUCTION

Bats (Mammalia: Chiroptera) are highly successful mammals with a molecular genomic origin hypothesized at about 63 Ma (Jebb et al., 2020). Their fossil record is improving and indicates they underwent an initial global radiation that resulted in at least eight archaic families (Onychonycteridae, Icaronycteridae, Archaeonycteridae, Palaeochiropterygidae, Philisidae, Hassianonycteridae, Mixopterygidae, Tanzanycteridae) in the early and middle Eocene. By the middle Eocene (48–38 Ma), the archaic bats were joined by an initial radiation of modern families and others (Emballonuridae, Hipposideridae, Necromantidae, Nycteridae, Rhinolophidae, Vespertilionidae; Sigé et al., 2012; Smith et al., 2012; Ravel et al., 2013, 2016; Hand et al., 2016; Hand and Sigé, 2018). Herein, we describe bats belonging to two archaic families and one modern family from a middle Eocene locality in western North America, dating to approximately 6 million years after the first appearance of chiropteran fossils (Smith et al., 2012).

All specimens presented in this work are from the Sheep Pass Formation, Eocene epoch, Bridgerian North American Land Mammal Age (NALMA), in Elderberry Canyon Quarry, near Ely, White Pine County, Nevada. Vertebrate fossils were discovered at Elderberry Canyon by Thomas D. Fouch in 1975 and were subsequently collected by Robert J. Emry and crews from 1976 to 1983 (Emry, 1990). Fouch (1979), studying the geology of Cretaceous and Paleogene rocks in the Great Basin, reported a fossil vertebrate, *Nyctitherium* cf. *velox*, from exposures of the Sheep Pass Formation in the Grant Range, another mountain range about 90–100 km southwest of the outcrops of the same formation in the Egan Range yielding the Elderberry Canyon vertebrates. Emry (1990) provided a vertebrate list consisting of around 40 taxa recovered from the Elderberry Canyon Quarry. Several of the mammals have already been reported, including about 30 taxa of insectivorous, carnivorous, condylarth, and hoofed mammals (Emry, 1990) and an unnamed apternodontid (listed in Asher et al., 2002:67–68), and detailed reports of the ceratomorph perissodactyl *Fouchia elyensis* (Emry, 1989), nine taxa of rodents (Emry and Korth, 1989), and the primate *Notharctus tenebrosus* (Perry et al., 2017) have been published. Additional mammals, amphibians, reptiles, and birds remain unstudied (Emry, 1990).

The Elderberry Canyon Quarry is in a limestone overlying a conglomerate approximately 50 m above the base of the local sequence of conglomerate and carbonate beds

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of the Sheep Pass Formation. The type section of the Sheep Pass Formation is in the southern Egan Range, where six members designated A–F are recognized (Fouch, 1979; Good, 1987). Elderberry Canyon Quarry is about 60 km to the north of the type section in the northern Egan Range and appears to be within Member E (Druschke et al., 2011).

The Elderberry Canyon local fauna is considered to reflect late early Eocene to earliest middle Eocene time by biochronologic correlation. The mammal fossils were originally recognized as having the greatest similarity to those of the Blacks Fork Member (or lower) of the Bridger Formation of Wyoming and other early Bridgerian localities (Emry, 1990). The Elderberry Canyon local fauna was later interpreted as representing subage Br2 by Robinson et al. (2004: table 4.1) and Janis et al. (2008: appendix I). However, an improving correlation web of western North American biochronological, geomagnetic, and radioisotopic age data modifies this age determination slightly. Perry et al. (2017:3) reaffirmed Emry's (1990) original faunal correlation, noting that the "Elderberry Canyon fossil assemblage most closely resembles that of the Blacks Fork Member of the Bridger Formation (Bridger A and Bridger B) (Emry, 1990; Murphey and Evanoff, 2011), now more commonly referred to as Bridger Biochrons Br1b and Br2 (respectively; see Gunnell et al., 2009[a])." In calibrating the early to middle Eocene Geomagnetic Polarity Time Scale with radiometric dating of the Bridger Formation and other formations in Wyoming, Tsukui and Clyde (2012) revised the correlation of Br1b and Br2. A Br2 (upper Blackforkian subage) fauna from the Grizzly Buttes locality, Wyoming, associated with the Church Butte tuff (Alexander and Burger, 2001) was previously correlated with magnetic chron C21r. Tsukui and Clyde (2012: table 2) revised the placement of the Church Butte tuff to the underlying chron C22n. The Ypresian–Lutetian stage/age boundary was placed at the reversal from C22n to C21r and was calibrated at 49.21 Ma in the Bridger Formation by Tsukui and Clyde (2012), whereas globally, Speijer et al. (2020) placed the same boundary within chron C21r rather than between C22n and C21r. According to the International Commission on Stratigraphy's (2021) International Chronostratigraphic Chart, the Ypresian–Lutetian boundary is dated as 47.8 Ma. Thus, by correlation with the Bridger Formation, Blacks Fork Member mammals and with the Geomagnetic Polarity Time Scale, the Elderberry Canyon local fauna is either near the Ypresian–Lutetian boundary or solidly within the Ypresian. Biochronologically, it fits within Bridgerian subage Br1b or Br2, which are consistent with magnetic chrons C22n–C21r, for which the radiometric age range is constrained between 50.11 and 48.03 Ma (Tsukui and Clyde, 2012: fig. 8). This correlation also suggests the Elderberry Canyon local fauna corresponds to the end of the Early Eocene Climatic Optimum (EECO; Zachos et al., 2001; Woodburne, 2004; Westerhold et al., 2020). Most of the Eocene interval represents a time when the Earth's climate was warm from the equatorial to the polar regions—the last such episode before the late Eocene–early Oligocene global cooling—and a time of high biodiversity (Gunnell, 2001; Cramwinckel et al., 2018). However,

during the Bridgerian this cooling transition began and, during the latter part of the EECO during Br1b–Br3, resulted in a major loss of the faunal diversity (Woodburne et al., 2009a; Cramwinckel et al., 2018).

Various tectonic, geochronologic, and isotopic data support a hypothesis proposing that the early middle Eocene landscape in which the Sheep Pass Formation was deposited and in which the Elderberry Canyon local fauna lived was part of a topographically high-standing region known as the Nevadaplano (Good, 1987; DeCelles, 2004; Druschke et al., 2011; Chamberlain et al., 2012; Loughney et al., 2021). A taphonomic and paleontological analysis of Members B (?uppermost Cretaceous–Paleocene) and C (Paleocene) of the Sheep Pass Formation also indicated that the type section of the formation (to the south of Elderberry Canyon in the same Egan Range) "represents a highland, cool water, alkaline, lacustrine setting on the Nevadaplano" (Bonde et al., 2020:18). A study of mollusks from the Sheep Pass Formation, Member E, in the type section at Sheep Pass Canyon (the same member that yielded the mammals at Elderberry Canyon Quarry) produced a high diversity of lung-bearing mollusks of the "Lymnaeidae–*Biomphalaria* association" that indicate a "shallow, ephemeral lacustrine environment with abundant emergent vegetation" within lacustrine limestones (Good, 1987:467).

One of the few previous records of a bat from the Bridgerian NALMA is of the icaronycterid *Icaronycteris* from the Green River Formation in Wyoming; the genus *Icaronycteris* extends from Wasatchian (late early Eocene; Wa7) into Bridgerian biochron Br3 (Czaplewski et al., 2008; Gunnell et al., 2009a; Smith et al., 2012). Another Bridgerian occurrence of a bat is a jaw fragment with m2 from the late Bridgerian "Hyopsodus Hill" locality, Tabernacle Butte area, Wyoming, in the Bridger Formation (McKenna et al., 1962:27, fig. 9). This specimen was described by the authors as having a striking resemblance to the recent vespertilionid *Eptesicus* (McKenna et al., 1962:29). Legendre (1985) tentatively considered the specimen a member of ?Molossidae but did not directly examine it. Finally, Brown (1959) initially reported a mandible, scapula, and humerus of an unidentified bat from the Nut Beds, Clarno Formation, Oregon, as Chadronian (late Eocene) in age, but the Nut Beds locality has more recently been tentatively assigned to the Bridgerian, Br3 (early middle Eocene), by Robinson et al. (2004). The purpose of the present study is to describe the Elderberry Canyon bats.

MATERIALS AND METHODS

All specimens described in this work are preserved in the collections of the Department of Paleobiology, National Museum of Natural History, and their catalog numbers are prefixed by the abbreviation USNM PAL. In the descriptions below, dental terminology follows Sigé et al. (2012), Smith et al. (2012), Hand et al. (2015), and Ravel et al. (2016). Tooth loci are indicated as standard for mammalian teeth, with upper case letters for upper teeth, lower case for lower teeth, I/i for incisors, C/c for canines,

P/p for premolars, and M/m for molars. All known bats retain no more than three lower premolars, reduced from four or five ancestrally; we follow the traditional system of labeling these p2, p3, and p4, assuming that p1 was lost in the immediate ancestry of bats (e.g., Smith et al., 2012; Hand et al., 2016). We compared the palaeochiropterygid specimen with casts of *Palaeochiropteryx tupaiodon* (HLMD 655 [Me 25] lectotype, HMLD 4271 [Me 26b], and HMLD 517 [Me 43] from Messel), *Palaeochiropteryx spiegelii* (HLMD 853 [Me 32] from Messel), and *Cecilionycteris prisca* (GMH 3965 and GMH 2884 from Geiseltal), as well as photographs and descriptions of other related genera in the published literature (Revilliod, 1917; Heller, 1935; Russell and Sigé, 1970; Sigé and Russell, 1980; Smith et al., 2012). Specimens of other taxa were also compared with casts and published illustrations and descriptions as cited herein. Fossils were photographed in iterative series at 25× magnification using a single-lens reflex camera with bellows and StackShot automated focus stacking rail and driver; resulting images were stacked with focus stacking software and masked and labeled with Photoshop software. The general surface view of the matrix block containing USNM PAL 417350 was photographed with an Android phone camera. Specimens were measured to the nearest 0.05 mm either using an ocular micrometer in a dissecting microscope calibrated with a stage micrometer or with the measuring tool in Adobe Photoshop software on photographic images originally made at 25× magnification. The small block of matrix containing the partial skeleton of USNM PAL 417350 was scanned at the MicroCT Imaging Consortium for Research and Outreach (MICRO; University of Arkansas, Fayetteville). The scan was performed on a 2018 Nikon XT H 225 ST μ CT system (Nikon Metrology, Brighton, Michigan, USA) at 33.75 μ m resolution (isometric voxels), using 150 kV, 130 μ A, 708 ms exposure timing, and 4× multiframe averaging, with a 0.25 mm aluminum filter, and on a tungsten target for 223 minutes.

ABBREVIATIONS

APL	anteroposterior length
ARK	archival resource key
Br0, 1, 2, 3	subchrons of the Bridgerian North American Land Mammal Age
C, c	upper, lower canine
Cf3	subchron of the Clarkforkian North American Land Mammal Age
EEOCO	Early Eocene Climatic Optimum
GMH	Geiseltal Museum, Halle, Germany
HLMD Me	Hessisches Landesmuseum, Darmstadt, Germany, Messel locality
I, i	upper, lower incisor
LF	local fauna
M, m	upper, lower molar
Ma	mega-annum; million years ago
MICRO	MicroCT Imaging Consortium for Research and Outreach, University of Arkansas, Fayetteville

MN	European Neogene Mammal chron
MP	European Paleogene Mammal chron
μ CT	micro-computed tomography
NALMA	North American Land Mammal Age
P, p	upper, lower premolar
PETM	Paleocene–Eocene Thermal Maximum
SALMA	South American Land Mammal Age
TW	transverse width
USNM PAL	United States National Museum, Paleobiology Department (National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA)
Wa7	subchron of the Wasatchian North American Land Mammal Age

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758

ORDER CHIROPTERA BLUMENBACH, 1779

FAMILY ?ONYCHONYCTERIDAE

Genus *Volactrix* gen. nov.

Volactrix simmonsae gen. et sp. nov.

FIGURES 1, 2; TABLE 1

HOLOTYPE. USNM PAL 544092, right dentary fragments with p2–m3.

PARATYPE. USNM PAL 417351, left dentary with p4–m3.

LOCALITY AND HORIZON. Elderberry Canyon Quarry in the Egan Range near Ely, White Pine County, Nevada, USA; Sheep Pass Formation, Eocene, Bridgerian NALMA.

ETYMOLOGY. Generic name from Latin *volo*, “fly,” and *actrix*, “doer, performer,” indicating flyer for the genus, and specific epithet for Nancy B. Simmons, in reference to her diverse, monumental, and epitomic research works and efforts on, and on behalf of, bats.

DIAGNOSIS. No other known Eocene bat has such a reduced, single-rooted p3 among three lower premolars (p2, p3, p4); p2 is relatively large, and p4 is reduced with a very small metaconid and short talonid. The hypoconulid on lower molars is relatively large and situated lingual to the midline but distinctly labial relative to the entoconid and lingual margin of molars (the postcristid configuration is intermediate between necromantodony and nyctalodonty). Further, *V. simmonsae* differs from *Palaeochiropteryx sambuceus* sp. nov. (described below) in its semimolariform p4 and from *Sonor handae* gen. et sp. nov. (described below) in having necromantodont–nyctalodont, rather than myotodont, lower molars.

DESCRIPTION

The holotype USNM PAL 544092 (Figure 1) has suffered multiple breaks, and the paratype USNM PAL 417351 (Figure 2) shows mesiodistal telescoping–compaction of the molars (but, enigmatically, not of the dentary bone), obscuring the hypoconulids, especially on m2, and affecting some measurements of these teeth (Table 1). These specimens represent a slightly larger and different taxon from *Palaeochiropteryx sambuceus* sp. nov. The statistical relationship between molar sizes and body weights in bats (Gunnell et al., 2009b) can be used to predict a body mass of about 11.6 g for *Volactrix simmonsae*. Measurements

are provided in Table 1. In the dentary a lateral mental foramen is visible between the c1 and p2 roots; the ascending ramus is broken off, but anterior parts of the coronoid process and masseteric fossa are preserved. The anterior edge of the coronoid process is nearly vertical (in the paratype; broken and displaced in the holotype). The ventral edge of the horizontal ramus is nearly straight in lateral view. The posterior portion of the mandibular symphysis is abraded but appears to have been unfused. In addition to the three molars in each specimen, the paratype preserves approximately the distal 1/3 of the c1 alveolus and p2 and p3 alveoli plus an intact p4, whereas the holotype preserves the intact p3 and broken p4. In the holotype the p2 is separated but



FIGURE 1. *Volactrix simmonsae* gen. et sp. nov., USNM PAL 544092, holotype dentary fragments with p2–m3 in labial (top), occlusal (center), and lingual (bottom) views (m, lower molar; p, lower premolar).

associated with the dentary, which is in two pieces, one piece preserving the minuscule p3, broken p4, and m1–m2 and the other piece preserving the m3 and a portion of the ascending ramus.

The three lower premolars consist of a relatively large p2, a very small p3, and a large, semimolariform p4. The p2 and p3 are single rooted, whereas the p4 is double rooted. The p2 (as preserved in the holotype) is moderate in size, about twice as long as wide and ovoid in occlusal view, slightly wider posteriorly than

anteriorly, and bears a simple cusp that is positioned mesially over the root, with a sharp posterior crest descending to a tiny cusplule on the cingulum. The cingulum enamel is broken labially, but the cingulum appears to have completely surrounded the base of the tooth. The p3 is tiny, with a circular outline in occlusal view, and its crown consists of a strong circular cingulum surrounding a low central cusp that is barely taller than the cingulum; this tooth is almost completely overhung by the posterior end of p2 and



FIGURE 2. *Volatrix simmonsae* gen. et sp. nov., USNM PAL 417351, paratype horizontal ramus with p4–m3 in labial (top), occlusal (center), and lingual (bottom) views (m, lower molar; p, lower premolar).

TABLE 1. Measurements (mm) of lower jaws and teeth of bats of the Elderberry Canyon local fauna, Nevada, middle Eocene, Bridgerian 2. Square brackets indicate the estimated measurement of a damaged specimen. A dash (—) indicates the measurement is not possible because of damage. Abbreviations: alv, alveolar measurement, not actual tooth dimension; APL, anteroposterior length; c, lower canine; L, length; lab, labial; ling, lingual; m, lower molar; p, lower premolar; TalW, talonid width; TrigW, trigonid width; TW, transverse width; W, width.

Measurement	<i>Volatrix</i>	<i>Volatrix</i>	<i>Palaeochiropteryx</i>	<i>Sonor bandae</i>
	<i>simmonsae</i>	<i>simmonsae</i>	<i>sambuceus</i>	<i>USNM PAL</i>
	USNM PAL	USNM PAL	USNM PAL	USNM PAL
	544092 holotype	417351 paratype	417350 holotype	544091 holotype
Depth of dentary at m1 back root alveolus, lab/ling	1.65/2.05	1.5/2.0	—/1.7	1.4/1.9
c1 APL	—	—	1.0	alv 0.75
c1 TW	—	—	0.6	alv 0.45
p2 APL	1.3	alv 0.6	0.7	alv 0.5
p2 TW	0.8	alv 0.55	0.5	alv 0.5
p3 APL	0.5	alv 0.25	0.95	alv 0.8
p3 TW	0.5	alv 0.3	0.65	alv 0.4
p4 APL	1.4	1.3	1.3	alv 0.9
p4 TW	0.95	0.9	0.7	alv 0.4
m1 APL	2.0	2.0	1.75	1.5
m1 TrigW	1.35	1.25	0.85	0.95
m1 TalW	1.25	1.25	1.0	1.05
m2 APL	1.9	2.0	—	1.42
m2 TrigW	1.8	1.25	—	1.05
m2 TalW	1.2	1.25	—	1.0
m3 APL	1.8	1.9	—	—
m3 TrigW	1.2	1.2	—	—
m3 TalW	0.9	0.9	—	0.62
Alveolar length of mandibular tooth row	—	[8.5]	—	[7.4]
m1–m3 length	[5.5]	5.2	[4.5]	—

anterior end of p4. The p4 is semimolariform, with its talonid wider but much shorter than the trigonid portion of the tooth. The paraconid is reduced to a low, small cuspid at the anterolingual corner at the base of an anterolingually directed crest. The metaconid is reduced to a small remnant on the crest descending posterolingually from the main cuspid (best seen in the paratype lingual view in Figure 2) and is situated about two-thirds of the length of the crest from the protoconid apex, while another small cusplule occupies the posterolingual terminus of the same crest. The posterior heel has a transverse basin steeply inclined labially, with a small cingular cuspid at the posterolingual corner of the tooth; labial and lingual cingula are moderately developed.

The m1 trigonid is relatively open, whereas the trigonids of m2 and m3 are more anteroposteriorly compressed; in m2 the paracristid even curves strongly. On m1 and m2 there are weak, tiny cingulids at the foot of the trigonid valleys; in m3 this area is obscured by crushing and glue. Labial cingula of the lower molars are complete and well developed. In the lower molars the

cuspid heights, listed from tallest to shortest, are protoconid, metaconid, hypoconid, paraconid, entoconid, and hypoconulid (in m3 the hypoconulid is about equal in height to the entoconid). Cristids obliqua are relatively short in m1–m2 and meet the posterior walls of the trigonids slightly labial to the notch in the protocristid. Entoconids are relatively tall and appear triangular in lingual view. Entocristids are nearly straight in occlusal view and do not align with hypoconulids except in m3. Hypoconulids of m1–m2 are large and low and are situated distinctly labial relative to the entoconids but lingual to the midline of the molars; they occur at the lingual ends of strongly curved postcristids. This postcristid-hypoconulid-entoconid configuration is intermediate between necromantodony (in which the hypoconulid is on the midline of the tooth and in a median position between the entoconid and the hypoconid; Sigé et al., 2012; Maitre, 2014) and nyctalodony (in which the hypoconulid is at or near the lingual margin of the tooth and distal to the entoconid, as illustrated by Sigé et al., 2012; Maitre, 2014; Hand et al., 2016). Thus, herein

the condition is termed “necromantodont–nyctalodont.” The m3 talonid is narrower but relatively longer than in m1–m2, with a postcrisid that is deeply notched between the hypoconid and hypoconulid and is straighter than the postcrisids in m1–m2 (in occlusal view). In m3 the hypoconulid is large and tall, about as tall as the entoconid, situated lingual to the entoconid, and separated from the entoconid by a small groove, showing the necromantodont–nyctalodont arrangement. The morphology of the posterolingual corner of the talonid of m3 (as seen in the holotype, Figure 1) is somewhat variable; the paratype (Figure 2) differs from the holotype in that the m3 hypoconulid is situated at the lingual edge of the tooth and merged with the entoconid such that the hypoconulid and entoconid are barely distinguishable and separated only by a minute groove. The hypoconulid and entoconid in the paratype m3 would merge given a small amount of wear and then would appear as a squarish posterolingual corner of the talonid without either cusp being distinguishable, in contrast to the same cusps in the holotype m3. Talonid basins of all three lower molars are shallow.

COMPARISONS

Volatrix simmonsae is tentatively referred to Onychonycteridae as the family, and its contained genera were revised and diagnosed by Smith et al. (2012) because it has three lower premolars, with p3 and p4 being more reduced than in most other archaic families; p4 with a small metaconid; lower molar trigonids that are increasingly mesiodistally compressed from m1 to m3; and m1–m3 that have a relatively short cristid obliqua and well-developed hypoconulid. However, it differs from the genera referred by Smith et al. (2012) to Onychonycteridae (*Onychonycteris*, *Eppsinycteris*, *Ageina*, and *Honrovits*) in having a vertical, rather than posteriorly tilted, coronoid process of the dentary; single-rooted, rather than double- or triple-rooted, p3; a p4 paracristid that is oriented anterolingually, rather than mesiodistally; and lower molars with the hypoconulid more lingually displaced from the midline (i.e., molars are transitionally necromantodont–nyctalodont), with the hypoconulid on m3 being less distally projecting. Sigé et al. (2012) noted the evolving configuration of the posterolingual area of lower molars in archaic bats from the primitive condition of necromantodonty to nyctalodonty and myotodonty, as well as the intergeneric and even intraspecific variability of this region in many fossil and living bats. They recognized this dynamism in several lineages, including intermediate conditions they termed “subnyctalodont.” They observed that one taxon that “illustrates the necromantodont type is *Necromantis* Weithoffer, 1887 itself . . . from the French Quercy Phosphorites . . . of Middle to Late Eocene age. . . . Among available *Necromantis* specimens, the hypoconulid is somewhat variable in position, most often occurring as an inflated median lobe . . . and in some specimens as large, but somewhat lingually shifted” (Sigé et al., 2012:461). The necromantodont–nyctalodont condition of the talonid in

V. simmonsae provides further evidence to support this evolutionary transition in a middle Eocene bat.

Volatrix simmonsae differs more greatly from the other known Eocene bats as revised by Smith et al. (2012) in the following ways: from icaronycterids in having p2 larger than p3; from archaeonycterids in having p3 single rooted and much smaller than p4 and p4 with a much less distinct paraconid and metaconid; from palaeochiropterygids in having p2 larger than p3, p3 very small and single rooted, p4 paraconid and metaconid much more reduced (similar to the degree seen in the palaeochiropterygid *Anatolianycteris*; Jones et al., 2018), and the lower molar entocristids unaligned with the hypoconulids; from *Stebelinia* in having p3 much smaller than p4, p3 smaller than p2, and p3 single rooted; from hassianycterids in having p2 larger than p3 and p3 very small and single rooted; and from mixopterygids in having molars with less lingually situated hypoconulids and the hypoconulid absent on m3. *Volatrix simmonsae* resembles the early Eocene vespertilionid *Premonycteris* (Hand et al., 2016) in the reduced and single-rooted p3 but differs in having an even more reduced p3, less molariform p4 (in particular, much more reduced metaconid), and necromantodont–nyctalodont molars. *Volatrix simmonsae* also resembles the approximately contemporaneous early middle Eocene (Tejedor et al., 2009; Woodburne et al., 2014) indeterminate chiropteran from Laguna Fría, Argentina (Tejedor et al., 2005), in having necromantodont–nyctalodont molars (those in the Argentinian specimens are nyctalodont), but all other dental and skeletal aspects of the Argentinian taxon are unknown. It differs from philisids in having the p3 present and from Paleogene and recent emballonurids, rhinolophoids, and rhinopomatids in having three lower premolars and a p4 that retains a metaconid. It cannot be compared with the early Eocene *Altaynycteris aurora* (family incertae sedis) of central Asia because the lower teeth of that species are unknown (Jones et al., 2021).

Among noctilionoids, the Elderberry Canyon *V. simmonsae* specimens differ from speonycterids in having a single-rooted p3, from noctilionids and mystacinids in having three lower premolars, from mormoopids in having a p4 that retains a metaconid and a higher coronoid process of the dentary, from phyllostomids in having a p4 with a metaconid, from thyropterids in its single-rooted p3, and from furipterids in its reduced p3 that is smaller than p2.

Among vespertilionoids, *V. simmonsae* differs from myzopodids in its p4 with a metaconid; from miniopterids in its small, single-rooted p3 and lower molars with a less lingually situated hypoconulid; from natalids in its small, single-rooted p3 and p4 with a metaconid; from molossids in having three lower premolars, with both anterior ones being single rooted, and in having the molar hypoconulid directly posterior to the entoconid; and from many species in having necromantodont–nyctalodont molars. It differs from vespertilionids in having necromantodont–nyctalodont lower molars rather than nyctalodont or myotodont molars (Gunnell et al., 2012).

FAMILY PALAEOCHIROPTERYGIDAE REVILLIOD, 1917**Genus *Palaeochiropteryx* Revilliod, 1917*****Palaeochiropteryx sambuceus* sp. nov.**

FIGURES 3–8; TABLES 1, 2

HOLOTYPE. USNM PAL 417350, partial skeleton. ARK: <http://n2t.net/ark:/65665/354abaace-b010-4c46-ab17-9cb85f12bd3e>.

REFERRED SPECIMEN. USNM PAL 706598, left dentary with p4–m3 (buried within the same small limestone block as USNM PAL 417350, revealed by μ CT scanning). ARK: <http://n2t.net/ark:/65665/3d2008079-6be5-422b-90d8-825c0f4be19>.

LOCALITY AND HORIZON. Elderberry Canyon Quarry in the Egan Range near Ely, White Pine County Nevada, USA; Sheep Pass Formation, Eocene, Bridgerian NALMA.

ETYMOLOGY. From Latin *sambuceus*, “of elder,” referring to the plants for which the type locality in Elderberry Canyon is named.

DIAGNOSIS. Upper molars (M1 and M2) have a shallow anterior ectoflexus and weak to absent posterior ectoflexus. P4 has a relatively strong and high anterolingual cusp; p4 is molariform with a complete trigonid, including a tall, well-developed metaconid and wide, short talonid. The infraorbital foramen is large and positioned over the anterolabial root of P4 and posterolabial root of P3. *Palaeochiropteryx sambuceus* differs from *P. spiegelii* in its smaller general size, narrower C1, taller metaconid on p4, and less acute lower molar cusps. It differs from *P. tupaiondon* in its taller anterolingual cusp on P4, shallower anterior ectoflexus of M1 and M2, and infraorbital foramen situated slightly more posteriorly. It differs from *Cecilonycteris prisca* in having a P4 with a stronger anterolingual cusp, a relatively smaller p4 but similar-sized m1, a p4 with a minute cuspule on the posterolingual crest (postmetaconid crest), and an m1 with a lingual cingulum at the base of the trigonid valley. It differs from *Matthesia* Sigé and Russell, 1980 in its smaller size, smaller and less robust C1, P4 having a stronger anterolingual cusp and narrower lingual (protoconal) lobe with deeper posterior emargination, M1 and M2 having weak metaconules, molariform p4 (with a metaconid and much stronger paraconid), and lower molars having less bulbous cusps. It differs from *Microchiropteryx* Smith et al., 2007 in its larger size and in having the hypoconulid of m1 more linguallly positioned. It differs from *Lapichiropteryx* Tong, 1997 in having upper molars with small talons, a P4 with a larger anterolingual cusp, and a molariform p4.

DESCRIPTION

The characteristics of *Palaeochiropteryx sambuceus* available in the Elderberry Canyon specimen agree with the familial diagnosis of Palaeochiropterygidae provided by Smith et al. (2012) in

the dental characters except that the p4 metaconid is large, as in the palaeochiropterygids *Palaeochiropteryx* Revilliod, 1917 and *Cecilonycteris prisca* Heller, 1935 (Sigé and Russell, 1980; Smith et al., 2012). Its dental dimensions are within the ranges of those of *P. tupaiondon* and *C. prisca* and smaller than those of *P. spiegelii*. On the basis of the statistical relationship between molar size and body weight in bats (Gunnell et al., 2009b), *P. sambuceus* had a body mass of approximately 13.8–14.1 g, compared to about 10.4 g for the European *Cecilonycteris prisca*. All elements except isolated teeth (but including the teeth in situ in the cranium and left dentary fragment) show crushing. In the cranium, crushing has included anteroposterior telescoping-compression of the upper teeth, affecting their appearance and some of their measurements (Table 2). In the block of limestone containing the holotype partial skeleton, in addition to the teeth retained in the cranium and the left dentary fragment located near the wing elements, there are several associated stray teeth: a small premolar (either right P2 or left p2 or possibly upper incisor) with an element of adherent jawbone stuck to the top of the crushed braincase and a left C1 sitting on the shaft of a crushed radius near a phalanx fragment or clavicle(?) (Figures 3, 4). Near the lower end of the prepared face of the block (relative to the catalog number written at the upper right of the prepared face, not visible in the μ CT scans, but at lower center in Figure 3) below the long bones and near a small, short finger(?) bone

TABLE 2. Measurements (mm) of USNM PAL 417350, *Palaeochiropteryx sambuceus* sp. nov., rostrum and upper dentition from Elderberry Canyon local fauna, Nevada, middle Eocene, Bridgerian 2. Note that some measurements of the upper teeth are probably abridged by anteroposterior distortion–compaction. Abbreviations: C, upper canine; M, upper molar; P, upper premolar.

Measurement	Value
Length of infraorbital canal	1.30
Length of maxillary tooth row (C1–M3 alveoli)	6.10
C1 anteroposterior length of alveolus	1.05
C1 main cusp height from lingual cingulum	1.30
P2 anteroposterior length of alveolus	0.60
P2 transverse width of alveolus	0.50
P3 anteroposterior length of alveoli	0.37
P3 transverse width of alveoli	0.55
P4 anteroposterior length	0.60
P4 transverse width	1.25
M1 anteroposterior length	1.70
M1 transverse width	1.60
M2 anteroposterior length	1.45
M2 transverse width	1.90
M3 anteroposterior length	1.10
M3 transverse width	2.20



FIGURE 3. *Palaeochiropteryx sambuceus* sp. nov., USNM PAL 417350, holotype partial skeleton in small limestone block (beige) supported by a plaster block (white). The skeletal elements (red brown) include the cranium at the left edge of the limestone block and articulated wing elements running from the cranium across the center of the limestone. Other scattered bones also are visible. Scale bars are in centimeters. See also Emry (1990: fig. 5).

segment are several more isolated teeth. These include a stray right canine (c1), a smaller premolar (left p2?), and a left p3 (Figures 3, 4, 5). Micro-computed tomography scanning revealed another bat jaw deep within the block containing the skeleton USNM PAL 417350. The jaw is a left dentary with p4–m3 and appears to belong to the same taxon as 417350 on the basis of

its similar size and molariform p4, so it is tentatively included in *P. sambuceus* as a referred specimen. The scan also shows the molars are crushed together mesiodistally like the teeth on the exposed maxillaries and dentary. However, because the unexposed dentary and the partial dentary exposed on the surface of the block are both left ones, two individual bats are preserved

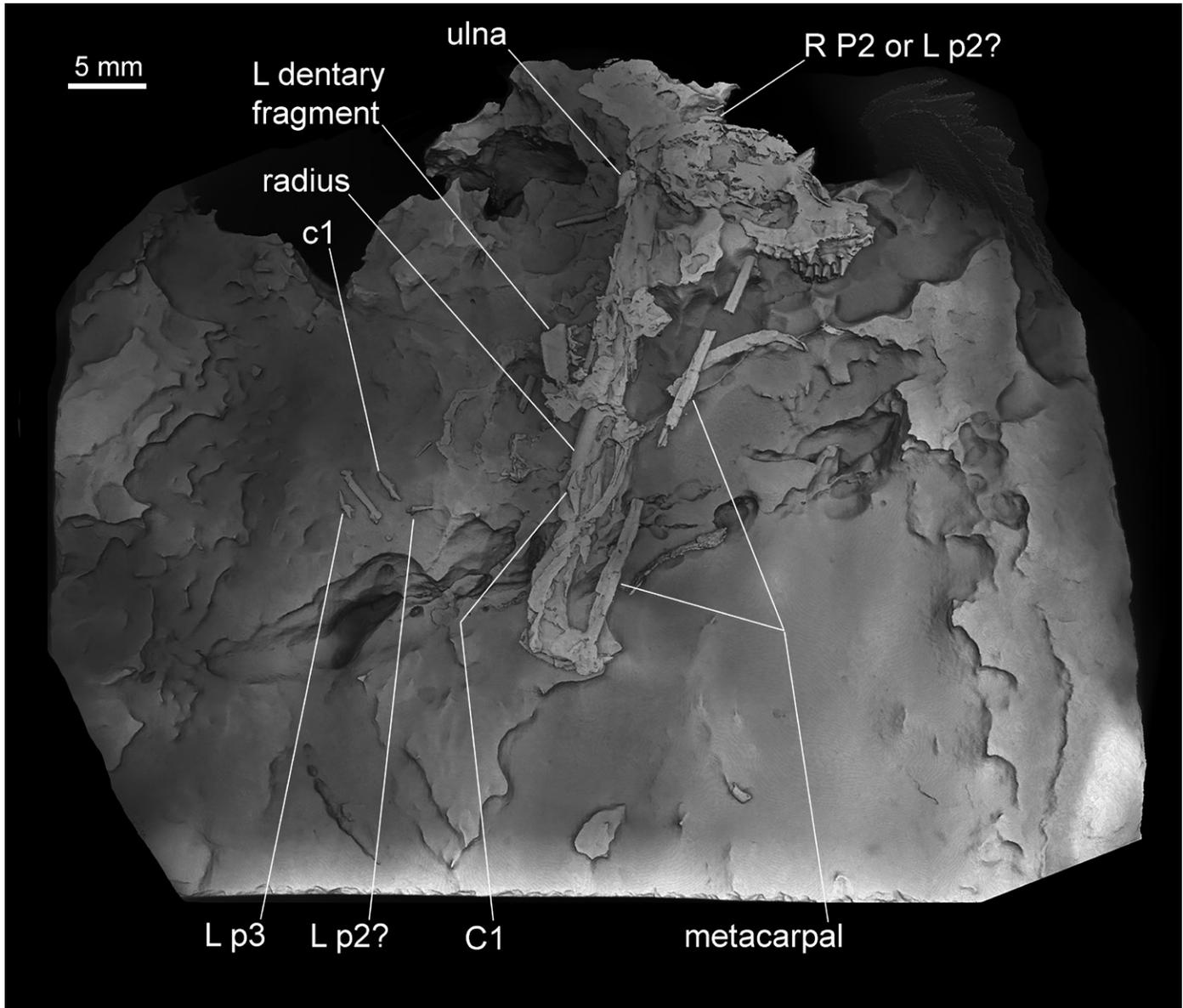


FIGURE 4. *Palaeochiropteryx sambuceus* sp. nov., USNM PAL 417350, holotype partial skeleton with partial cranium, left dentary fragment (enlarged in Figures 5, 7), scattered teeth, and appendicular elements in a small block of acid-prepared limestone matrix. Micro-computed tomography model, surface scan of block. Abbreviations: L, left; R, right; c/C, lower/upper canine; p/P, lower/upper premolar.

in the block, potentially calling into question whether the other exposed skeletal elements assigned to USNM PAL 417350 might belong to more than one individual.

CRANIUM. The anterior end of the cranium, including the premaxillaries and incisors, is missing in addition to the anterior teeth, but the canine and anterior premolar alveoli are preserved in the crushed maxillaries (Figure 6). The left and right sides of the cranium are somewhat displaced relative to one another. The braincase is flattened and shattered, rendering it

uninterpretable. Despite the absence of the premaxillaries, using the position of the canines and extrapolating the missing length of the rostrum, we infer different proportions of the rostrum relative to the braincase compared to *C. prisca* and *Palaeochiropteryx*: in the European taxa the facial cranium and braincase are described as being about equal to one another in length (Heller, 1935; Sigé and Russell, 1980), whereas in *P. sambuceus* the rostrum seems to have been much shorter than the braincase. As in *C. prisca* and *Palaeochiropteryx* (Heller, 1935; Sigé and

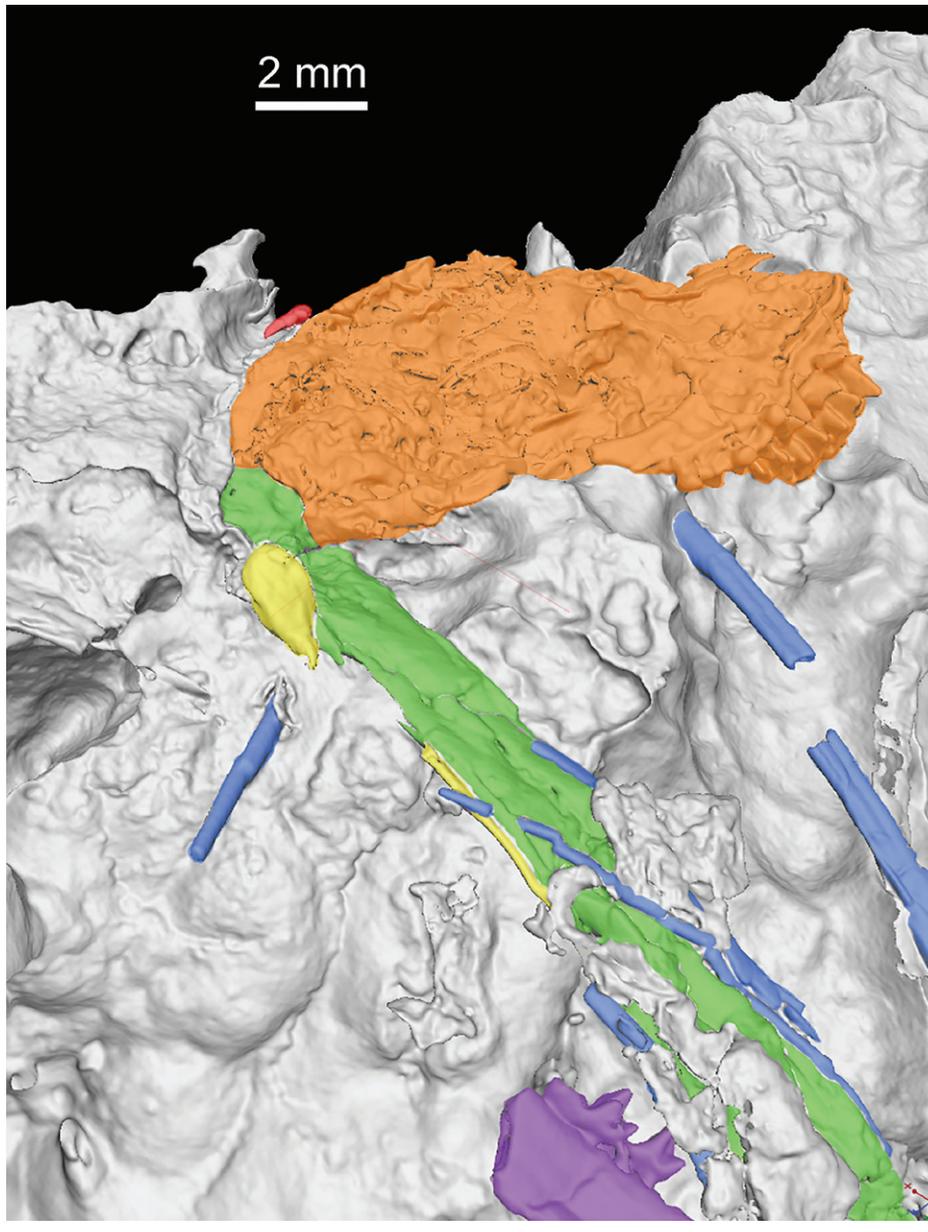


FIGURE 5. *Palaeochiropteryx sambuceus* sp. nov., USNM PAL 417350, holotype. Detail of μ CT surface model with selected elements colored as follows: red, right P2 or left p2; orange, cranium; yellow, ulna; green, radius; blue, metacarpal and phalangeal fragments; violet, left dentary fragment with p4–m1 (m, lower molar; P/p, upper/lower premolar).

Russell, 1980), the rostrum is low, and the forehead profile rises gradually from it (Figures 4, 5). The anterior edge of the orbit reaches the level of the anterior end of M2. The anterior base of the zygomatic arch arises at a level above the contact point of M2 and M3 and is relatively deep but quickly narrows. The infraorbital foramen is single, oval, and large, opening above the level of the posterolabial root of P3 and anterolabial root of P4.

Its vertical diameter is about equal to the distance from its lower rim to the posterior alveolus of P3, which is less than the span of the bridge over the infraorbital canal. The infraorbital foramen vertical diameter is 0.8 mm; the distance from the lower anterior orbital rim to infraorbital foramen is 1.45 mm. The infraorbital canal is relatively long (1.3 mm), its posterior opening is just out of lateral view inside the anteroventral rim of the orbit, above

the level of the posterior portion of M1, and its anterior opening is above the P3–P4 contact. As in other *Palaeochiropteryx* species, there is a small knob-like postorbital process at the dorsal end of the orbital rim. The dorsal surfaces of the nasal region do not appear to show evidence of shallow longitudinal grooves between the nasals or between the nasals and maxillaries. No sagittal crest can be detected in the shattered braincase.

UPPER DENTITION. The upper tooth rows are crushed mesiodistally, crowding adjacent teeth into one another and distorting their individual shapes somewhat (Figure 6), which should be taken into account when viewing the images and reading the word descriptions. The dental formula is

$\text{?I/i} - 1\text{C}/1\text{c} - 3\text{P}/3\text{p} - 3\text{M}/3\text{m}$; the premolar alveolar formulas are $\text{P2} = 1 \text{ alveolus}/\text{p2} = 1 \text{ alveolus}$, $\text{P3} = 3 \text{ alveoli}/\text{p3} = 2 \text{ alveoli}$, $\text{P4} = 3 \text{ alveoli}/\text{p4} = 2 \text{ alveoli}$. The cranium shows right and left P4–M3 and alveoli for C1, P2, and P3. The C1 alveolus is relatively small. The stray C1 is fairly robust, with a relatively horizontal cingulum except at the anterolingual and posterolingual corners, where it rises slightly toward the summit of the main cusp, with the posterolingual rise formed into a small cusp. The crown appears longer than wide, with a rather sharp posterior crest. The P2 alveolus is small and single, whereas the P3 is intermediate between P2 and P4 in size and had three roots. The P4 is relatively wide, with a tall main cusp, large anterolingual cusp

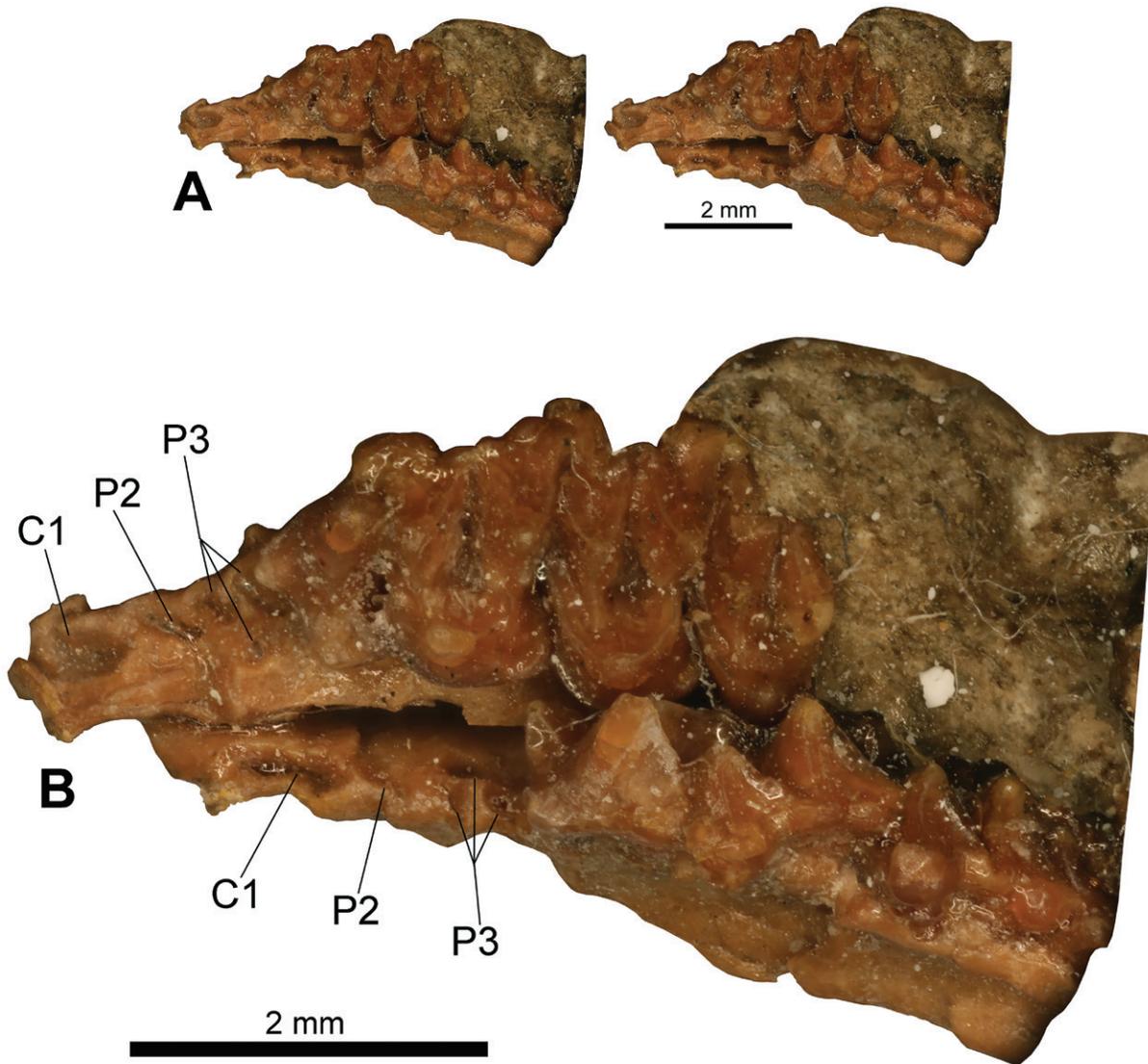


FIGURE 6. *Palaeochiropteryx sambuceus* sp. nov., USNM PAL 417350, holotype, (A) stereopair and (B) close-up detail of the palatal region and upper teeth in occlusal view. The specimen is heavily coated with consolidant. The bat's right-side teeth are rotated toward the midline by postdepositional processes. Canine (C1) and premolar (P2 and P3) alveoli are labeled in B.

on a narrow, rounded lingual lobe, and a low anterolabial cusp projecting anteriorly on the anterior lobe. The lingual lobe is separated from the posterolabial lobe by an indentation, making the lingual lobe appear “pinched.” There is a moderate labial cingulum. From the P4 anterolingual cusp, a crest extends labially to the anterolabial cusp, another extends around the lingual lobe of the tooth and posteriorly before disappearing where crowded against M1, and a slightly weaker crest extends across a small saddle-like area toward the main cusp. The strong high crest extending posterolabially from the main cusp toward the parastyle of M1 is jammed into the M1 on both sides of the rostrum, and thus, only the part adjoining the tip of the main cusp is visible. The M1 is narrower transversely than the M2. In all three upper molars the mesostyle occurs at the labial border of the tooth and appears to be doubled or slightly divided (centrocrista is separated labially). The labial margins of M1 and M2 retain short segments of the labial cingulum adjacent to the parastyle and mesostyle and across the opening of the metafossa anterior to the metastyle, but this cingulum is interrupted at the labial end of the parafossa and on the metastyle. The anterior ectoflexus is acute and moderately deep, whereas the posterior one is essentially absent in M1 and shallow in M2. The lingual cingulum is complete in M1 and M2 and thicker posterolingually, where it forms a very small talon with no true hypocone but a minuscule, abrupt rise along the lingual edge of the talon cingulum in each molar. From the protocone the preprotocrista extends anterolabially as a wide precingulum to the parastyle. The parastyle is large and hooked. The postprotocrista curves posteriorly to a small rise, forming a weak metaconule, which becomes sinuous or angled as a thin metaloph before contacting the base of the metacone. This crest complex is only slightly separated from the postcingulum, which is farther separated from the small talon. A paraconule is absent, but a long, strong paraloph extends from the base of the paracone toward the protocone but does not reach it. The profossa (trigon basin) is moderately deep, whereas the parafossa and metafossa are very shallow. M2 is transversely wider than M1. The M3 ectoloph has three commissures plus a very short postmetacrista; the postparacrista is of equal length to the premetacrista, and the parastyle is large and hooked. In M3, the postprotocrista is continuous with the metacingulum and separate from the posterior portion of the lingual cingulum. A paraconule is absent, but a strong paraloph occurs as in M1 and M2.

DENTARY AND LOWER DENTITION. The stray c1 seems to be missing some of its enamel, thus appearing to lack a labial cingulum, but this might be an artifact of preservation. It has a low and relatively small main cusp, a prominent anterolingual cusp that would have been adjacent to the lower incisors, and a notably small posterior basin and posterolingual cuspid. The stray p3 has two stout roots, anterior and posterior (the anterior is broken off). Like the c1, the crown is also missing enamel along the labial cingulum, or else the cingulum is abraded away, but it appears to have been fairly strong, and there appears to have been a slight rise along the labial cingulum at a level between the two roots. The p3 is much longer than wide and

bears no trigonid but has the main cusp connected by a ridge to an anterolingual cingular cusp; posteriorly, it shows a tiny heel with a small basin and a posterolingual cusp that is smaller than the anterolingual cusp.

The left dentary fragment preserved near the radius shows p4 and m1, two empty premolar alveoli (for the p3?) ahead of p4, and the root of a c1(?) behind some stray bits of bone and glue (Figures 3, 4, 5, 7). The two teeth in the lower jaw fragment are broken but not as distorted as the uppers. The p4 is clearly molariform, with a trigonid and a small talonid (Figure 7). The p4 has well-developed protoconid, paraconid, and metaconid as tall as those on the m1, with the paraconid being low and the metaconid being about two-thirds the height of the protoconid. All of the cusps are thin and narrow. The protoconid and metaconid are transversely aligned and closer together than the protoconid and paraconid, and the paraconid angles anterolingually. The p4 shows a minute cuspid low on the crest descending the posterior edge of the metaconid, a lingual cingulum restricted to the foot of the trigonid valley, and an anteroposteriorly short talonid with a small basin and single posterior cusp. The m1 trigonid is open, with a tiny lingual cingulum at the foot of the trigonid valley; the talonid is long and wider than the trigonid, and the talonid basin is wide and rather shallow and is occupied by a small chunk of stone or bone that obscures the cristid obliqua. The m1 hypoconulid is low and lingually situated almost at the lingual margin of the tooth and is separated by a tiny notch from the entoconid; the entoconid is broken off, and the hypoconulid also appears to be broken posteriorly. The postcristid is nyctalodont, although it is partly obscured by a film of glue. In the uncataloged, referred left dentary that is buried within the block containing USNM PAL 417350, the μ CT scan and movie files show its p4 also has a molariform trigonid with a relatively strong metaconid and a small talonid (Figure 8). Unfortunately, the molars in this dentary are crushed together, obscuring their morphological details.

POSTCRANIALS. Aside from the skull, the holotype specimen preserves parts of one wing, possibly the right (Figures 3, 4, 5). Like the craniodental parts of the specimen, the wing elements are crushed, fractured, distorted, and obscured, masking the anatomical features; only crude interpretations are possible. No portion of the axial skeleton seems to be exposed, except possibly for linear bits of ribs, although some of those pieces might be metacarpal and manual phalanx fragments. A large and long bone extending from beneath the back of the braincase is interpreted as the radius because the proximal epiphysis of the ulna with the olecranon process appears near its end lying close to the braincase where the elbow would be expected, and the proximal end of a metacarpal is preserved at the opposite end of this large bone where the wrist would be expected (Figures 4, 5 [green shading]). The radius is about 33 mm long, at the lower end of the range of radius lengths for *P. tupaiodon* from Messel, Germany, and shorter than those of *P. spiegelii* (Sigé and Russell, 1980), and does not appear to have had a pronounced curvature. The proximal epiphysis of the ulna appears near the proximal

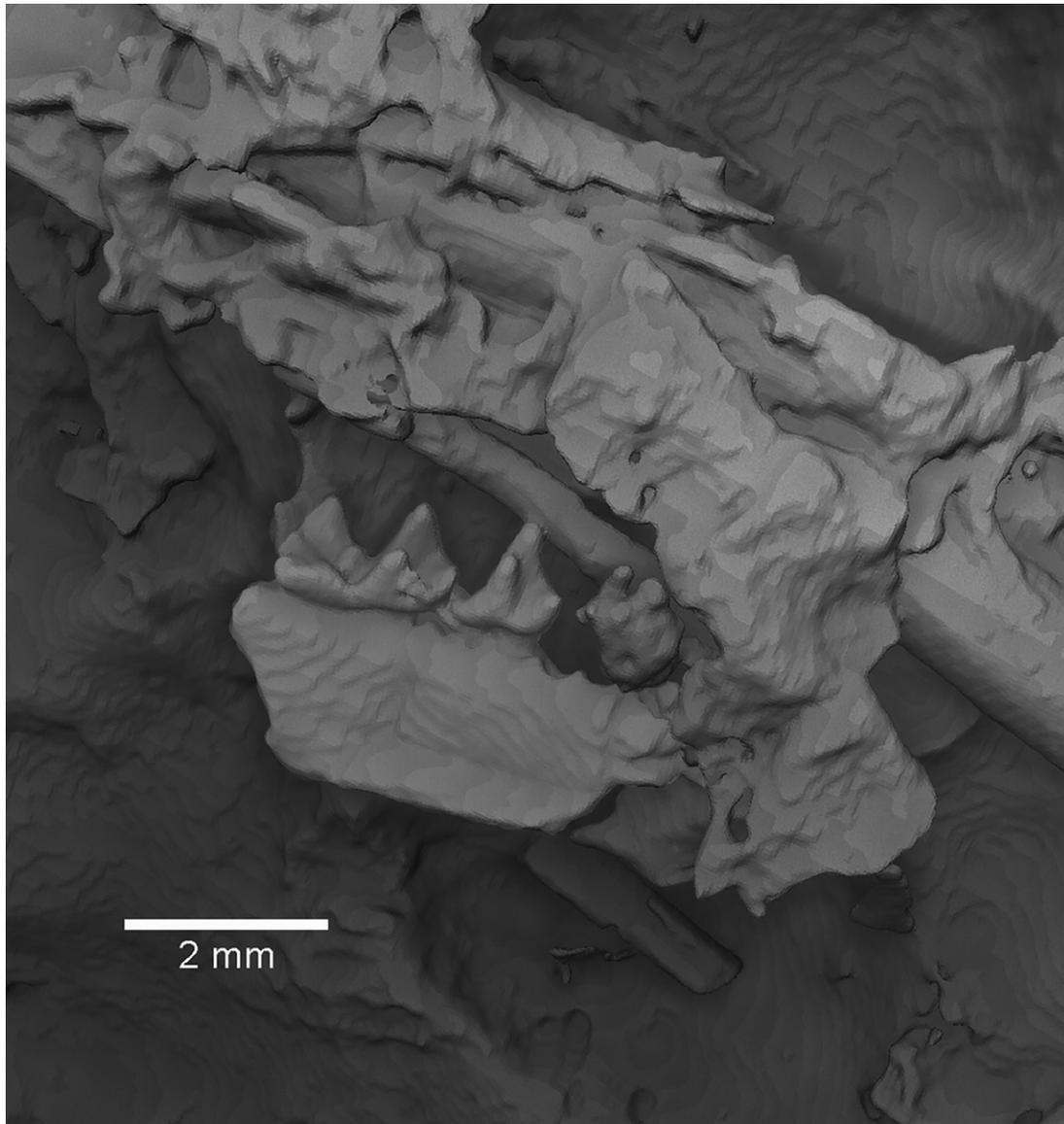


FIGURE 7. *Palaeochiropteryx sambuceus* sp. nov., USNM PAL 417350, holotype, μ CT surface model close-up of the left dentary fragment with p4–m1 and parts of nearby postcranials (m, lower molar; p, lower premolar). Note the well-developed trigonid of p4.

end of the radius (at the end near the cranium) and is separated from the thin ulnar shaft by a short gap (Figure 5, yellow shading). The articular surface of the ulna faces toward the cranium and cannot be examined directly. The shaft of the ulna is ossified, but its length and point of fusion with the radius cannot be determined because the shaft is covered by a rib head and bony debris along the middle portion of the radius. At the distal end of the radius, carpals are not discernible, but the proximal end of one of the larger metacarpals (metacarpal III? with a large, rounded

proximal epiphysis) is present, and separated segments of its shaft extend toward the cranium (Figures 4, 5 [blue shading]).

COMPARISONS

Palaeochiropteryx sambuceus differs from Onychonycteridae, Icaronycteridae, Archaeonycteridae, Hassianycteridae, and Mixopterygidae in dental characters provided in the diagnoses for these families by Smith et al. (2012). It differs from Vespertilionidae, including the early Eocene vespertilionid *Premonycteris*

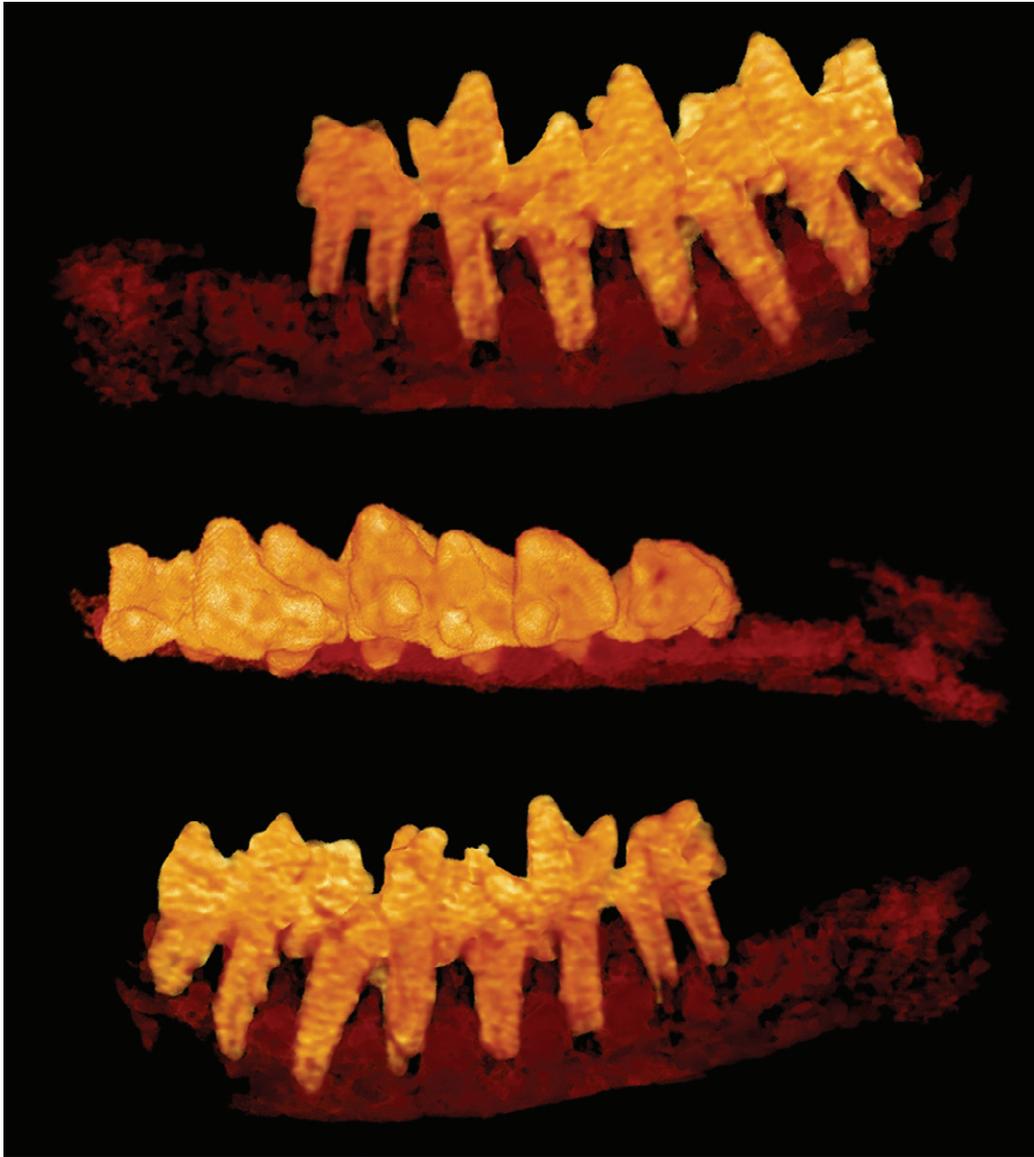


FIGURE 8. Image rendered from μ CT scans of a left dentary with p4–m3, tentatively referred to *Palaeochiropteryx sambuceus*, buried within the same small block of limestone that holds USNM PAL 417350 (m, lower molar; p, lower premolar). From top to bottom: labial view, occlusal view, lingual view.

vesper, in its two-rooted p3, better-developed trigonid on p4, and nyctalodont molars (Hand et al., 2016). Although few comparisons can be made because of preservation problems, at least the m1 of *P. sambuceus* resembles lower molars of the indeterminate chiropteran from Laguna Fría, Argentina, of about the same age as the Elderberry Canyon LF in its nyctalodontology and wide talonid basin (Tejedor et al., 2009), but the m1 of *P. sambuceus* is smaller than the Argentinian molars.

Palaeochiropteryx sambuceus differs from confamilial *Matthesia* in having p4 with a metaconid. Russell and Sigé (1970:87)

amended Revilliod's (1917) original diagnosis of *Palaeochiropteryx* to include, among other characters, "Métaconide de p4 inférieure de développement variable, mais toujours present" (metaconid of p4 of variable development, but always present). Smith et al. (2012:38) indicated that one of the diagnostic characters of the family Palaeochiropterygidae is "p4 metaconid small to nearly absent," whereas in *C. prisca* the p4 bears a strong and tall metaconid (Heller, 1935; Sigé and Russell, 1980). In a cast of the lectotype of *P. tupaiodon* from Messel (HLMD Me 25 [655], also illustrated by Russell and Sigé, 1970: plate I,

fig. 1), the p4 shows a strong metaconid. We agree with Smith et al. (2012) that *Cecilionycteris* appears to be a junior synonym of *Palaeochiropteryx* in the osteological characters of both genera currently known but requires more complete specimens preserving comparable elements to evaluate and formally synonymize. *Palaeochiropteryx sambuceus* differs from *C. prisca* in having a relatively smaller p4 (anteroposterior length 1.04 mm compared to 1.28 mm) while still having similarly sized m1s as well as an apparently shorter rostrum relative to the length of the braincase. For example, the anterior edge of the orbit is at the level of the anterior end of the M2, whereas in *C. prisca* it is much farther forward, at the posterior root of P4 (Sigé and Russell, 1980). The upper canine of *P. sambuceus* is similarly proportioned and stout like that of *P. tupaiodon*, *P. spiegelii*, *C. prisca*, and *Matthesia germanica* (Russell and Sigé, 1970; Sigé and Russell, 1980) but is smaller and possibly transversely narrower than C1 in *P. spiegelii* and *M. germanica*. It is within the size ranges of C1s of *P. tupaiodon* and *C. prisca* (compare with measurements in Sigé and Russell, 1980). Notches in the labial borders of the M1 and M2 on either side of the mesostyle (i.e., anterior and posterior ectoflexi) have been used to distinguish these genera and species (Russell and Sigé, 1970; Sigé and Russell, 1980); however, this characteristic might be subject to individual variability. In M1 the anterior ectoflexus (posterior ectoflexus) in each species is as follows: *P. sambuceus*, shallow (absent); *P. spiegelii*, deep (absent); *P. tupaiodon*, deep (absent); and *C. prisca*, deep (shallow). In M2 the anterior ectoflexus (posterior ectoflexus) in each species is as follows: *P. sambuceus*, shallow (absent); *P. spiegelii*, deep (shallow); *P. tupaiodon*, deep (absent); and *C. prisca*, deep (unknown, broken in the holotype).

Postcranially, the skeleton in palaeochiropterygids is known only in *P. tupaiodon* and *P. spiegelii* and partially in *C. prisca* from Germany and France. The relative lack of curvature of the radius in *P. sambuceus* is similar to that in *P. tupaiodon* (e.g., Smith et al., 2012). The length of the ulna (if complete) is shorter than in *P. tupaiodon* (Smith et al., 2012: fig. 2.7). It also differs from *Icaronycteris index* and *Onychonycteris finneyi*, in which the ulna shaft fuses with the radius much more distally, distal to the midpoint of the ulna (Jepsen, 1966: fig. 1; Simmons et al., 2008: fig. 1 and supplementary information p. 19).

SUPERFAMILY VESPERTILIONOIDEA GRAY, 1821

FAMILY VESPERTILIONIDAE GRAY, 1821

Genus *Sonor* gen. nov.

Sonor handae gen. et sp. nov.

FIGURE 9; TABLE 1

HOLOTYPE. USNM PAL 544091, left dentary with m1–m3, only known specimen.

LOCALITY AND HORIZON. Elderberry Canyon Quarry in the Egan Range near Ely, White Pine County, Nevada, USA; Sheep Pass Formation, Eocene, Bridgerian NALMA.

ETYMOLOGY. Latin *sonus*, “noise, sound,” suggesting “caller” and assuming that the bat used echolocation. The species is named for Suzanne Hand, a paragon of a paleontologist, biogeographer, student, and teacher of the evolution of bats and many more vertebrates of Australia, New Zealand, and beyond.

DIAGNOSIS. The combination of three uncrowded lower incisors, a two-rooted p3 larger than p2, and myotodont lower molars distinguishes *Sonor handae* as a new taxon of Vespertilionidae. It differs from all archaic bat families, most Eocene bats, and extinct and extant miniopterids in having lower molars with myotodont postcristids. It differs from the early Eocene vespertilionid *Premonycteris vesper* in having a two-rooted, rather than one-rooted, p3 and lower molar labial cingula that rise up on the base of the protoconid. In having a two-rooted p3, *S. handae* resembles the latest Eocene vespertilionid, *Khonsunycteris aegypticus* of Egypt, but differs in that the p3 roots are in line with the long axis of the tooth row, not angled in the dentary. The Elderberry Canyon fossil differs from the European Eocene and Oligocene *Stehlinia* and the Oligocene and Miocene *Quienetia* in having myotodont lower molars. USNM PAL 544091 differs from the European Miocene *Hanakia* and from extant myotodont vespertilionids in having a two-rooted p3. It most closely resembles extant kerivoulines *Kerivoula* and *Phoniscus* in most aspects of lower premolar and molar morphology but differs in having larger molars relative to the size of the premolars.

DESCRIPTION

On the basis of molar size (Table 1) and its correlation with body mass (Gunnell et al., 2009b), *S. handae* had a body mass of approximately 17.3–20.3 g. The left dentary is in two pieces showing the three molars and empty alveoli for most other teeth. One piece includes most of the horizontal ramus with m1–m2 and alveoli for all anterior teeth (Figure 9), and the second piece with the posterior end of the ramus includes the talonid of m3 but no part of the ascending ramus. The edentulous part of the horizontal ramus is crushed but shows alveoli for three lower incisors; c1; and five alveoli for three premolars, including a single-rooted p2, double-rooted p3, and double-rooted p4. The mandibular symphysis is unfused. Although the premolars themselves are missing, their alveoli indicate that lower premolar size increases from p2 to p4. The incisor alveoli are empty except for i2, which holds the broken root. Crushing interferes with interpretation, but the incisor alveoli appear not to be compressed or crowded, differing from the condition in many extant vespertilionids with three lower incisors in which the crowns are aligned but the roots are slightly staggered. The p2 alveolus is relatively the largest premolar alveolus and rounded in occlusal view, p3 alveoli are the smallest and squarish, and p4 alveoli are each slightly larger than the p3 alveoli but not as large as the single p2 alveolus and

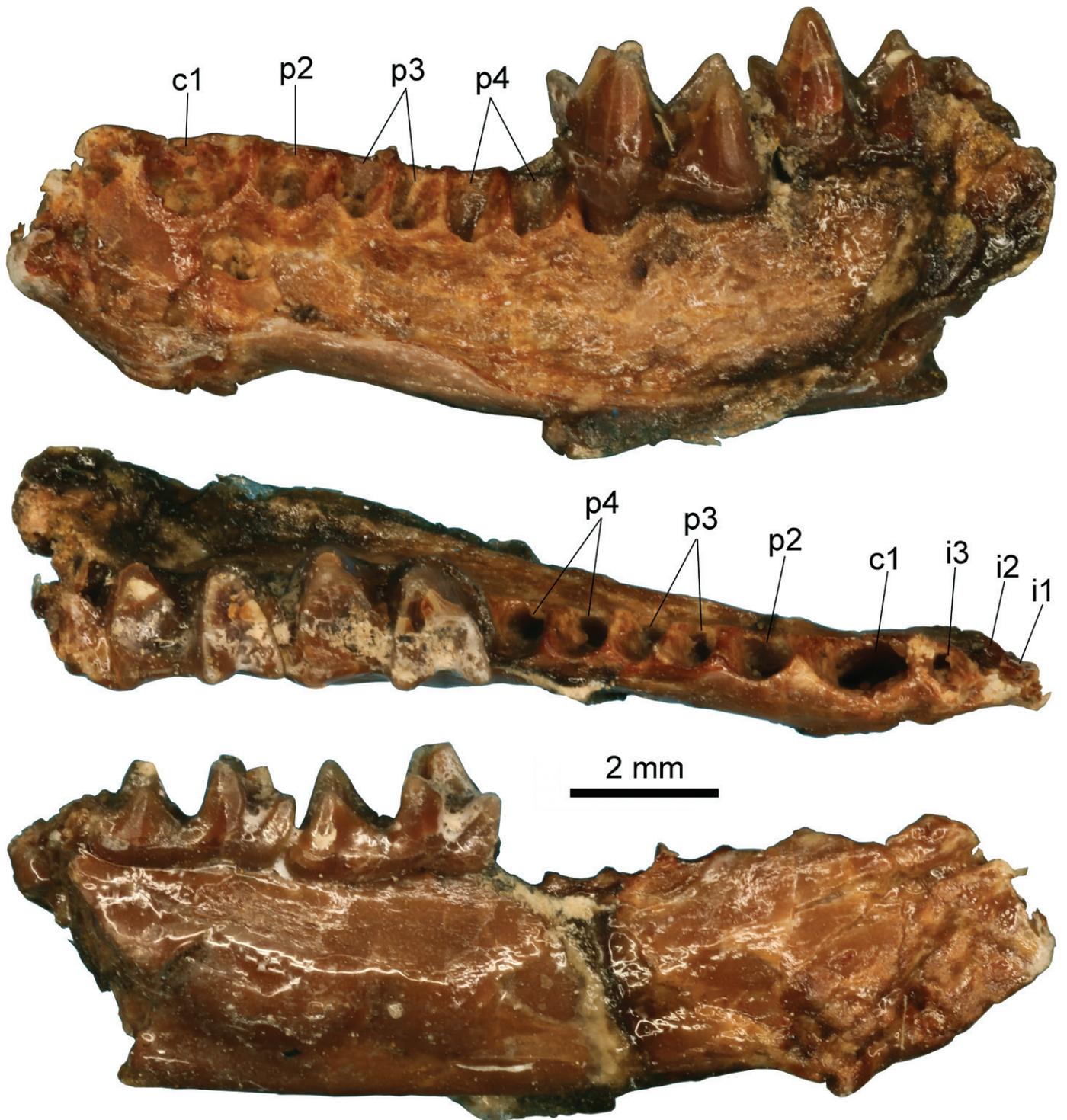


FIGURE 9. *Sonor bandae*, USNM PAL 544091, holotype left dentary with m1–m2 and partial m3, in labial, occlusal, and lingual views from top to bottom. Tooth loci are indicated for the empty alveoli. Abbreviations: c, lower canine; i, lower incisor; m, lower molar; p, lower premolar.

squarish. A small mesial mental foramen opens ventral to the i1 alveolus and near the symphyseal line, and a large lateral mental foramen opens on the side of the ramus between the roots of c1 and of p2. The m1 and m2 are clearly myotodont, with a low, but relatively long, hypoconulid directly behind the entoconid and at the lingual margin of the tooth. The m1 trigonid is moderately open, whereas that of m2 is more anteroposteriorly compressed. There are no lingual cingulids at the bases of the trigonid valleys. Labial cingula are complete and strong around the trigonids, where they rise slightly but distinctly up onto the labial bases of the protoconids, but the cingulum is weaker around the bases of the talonids. The cristid obliqua is sinuous in m1 but straight in m2. Entoconids on m1 and m2 are tall and triangular in lingual view, with high, straight entocristids in occlusal view. Only fragments of the m3 are preserved in the second piece of the specimen, but the talonid is relatively large, shows myotodony, and bears a distinct small hypoconulid separate from the entoconid, which is broken.

COMPARISONS

Sonor handae is most similar to the Kerivoulinae among vespertilionids in several characteristics. In particular, the lower incisor row is not compressed, the p3 is double rooted, and the molars are myotodont (Horáček, 1988). *Sonor handae* differs from *Kerivoula* and *Phoniscus* in having more of a gradation in lower premolar size with $p2 < p3 < p4$ rather than $p2 = p3 < p4$ and in having the molars relatively large compared to the premolar row (as implied by the size of empty alveoli).

FAMILY INDETERMINATE

MATERIAL. USNM PAL 544095A, left upper canine; USNM PAL 544093, distal humerus fragments; USNM PAL 544094, limb bones and fragments embedded in a wafer of glue.

USNM PAL 544095A consists of approximately 17 pieces, including an edentulous dentary and many isolated teeth, most of which appear to be soricomorphs or other taxa; the "A" added to the specimen number is our designation for what appears to be the only bat tooth in the lot, a left C1 (Figure 10). The canine is missing the tip of its main cusp. In occlusal view it bears a straight lingual border associated with the flat lingual face of the main cusp, a flat anterior face, and a rounded labial margin. The cingulum maintains a constant level and strength around most of the base of the tooth except at the posterolingual corner, where the cingulum drops and forms a small, sharp secondary cuspule at the junction with a sharp posterolingual crest running from the apex of the main cusp. The root is stouter than the crown. Its measurements, in millimeters, are C1 APL, 1.1; C1 TW, 0.85; and C1 cusp height from lingual cingulum, broken, estimated at 1.5.

Most pieces of the humerus USNM PAL 544093 are shaft fragments; the only recognizable piece is a crushed distal end with the anteroposteriorly flattened epiphysis (Figure 11). The



FIGURE 10. Chiroptera indet., USNM PAL 544095A, left upper canine in anterior, labial, occlusal, posterior, and lingual views from left to right.

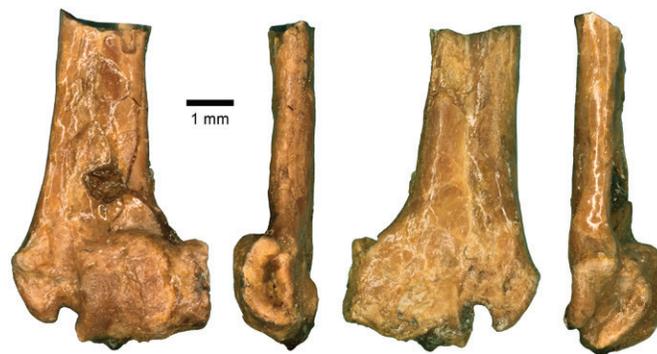


FIGURE 11. Chiroptera indet., USNM PAL 544093, distal humerus fragment in anterior, lateral, posterior, and medial views from left to right.

crushing distorts many proportions, but the distal articular surface is clearly offset laterally from the humeral shaft. There is a broad medial epicondyle with a spinous process separated by a wide notch from the medial edge of the trochlea; the spinous process extends distad but does not reach the distal extent of the trochlea. Crushing interferes with observation, but there does not appear to have been an olecranon fossa posteriorly or a strong radial fossa anteriorly. Humeral measurements are provided in Table 3.

This element has a general resemblance to the distal humerus of Eocene bats of many taxa, including at least *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, palaeochiropterygids (*Palaeochiropteryx* and *Cecilionycteris*), *Stebliina*, and *Vespertiliavus*, as well as members of many recent taxa, including Yinpterochiroptera, Phyllostomidae, some Mormoopidae, Noctilionidae, Natalidae, Myotinae, Murininae, and Kerivoulinae (Simmons and Geisler, 1998). Indeed, Simmons and Geisler (1998) considered the laterally displaced articular surface configuration primitive

TABLE 3. Measurements (mm) of USNM PAL 544093, Chiroptera indet., distal humerus fragment from Elderberry Canyon local fauna, Nevada, middle Eocene, Bridgerian North American Land Mammal Age.

Measurement	Value
Humerus shaft transverse diameter	1.9
Distal transverse width	4.1
Extension of trochlea beyond spinous process	0.4
Proximodistal diameter of trochlea	2.1
Transverse width of medial epicondyle	1.3
Width of distal articular surface	2.8

for bats and contrasted it with bat humeri in which the articular surfaces are in line with the shaft (some Emballonuridae, some Mormoopidae, Mystacinidae, Miniopteridae, Molossidae, Vespertilioninae, and some Myotinae). The degree of lateral displacement varies among these groups, and the isolated distal humerus from Elderberry Canyon is moderate in its displacement. It is less displaced than in *Cecilionycteris* and has a strong hooklike spinous process on the epitrochlea; it could belong to any of the named taxa discussed in this report, including, potentially, the vespertilionid *S. handae* if it proves to belong to Kerivoulinae.

The only distal epiphysis of the humerus available to Heller (1935:307) for *C. prisca* was said to be not well preserved but was described as being broad and strong, in the front view showing a slightly spherical capitulum, narrow cylindrical trochlea, and “einer schlecht erhaltenen Epitrochlea” (poorly preserved epitrochlea) but “von einem dornförmigen Epicondylus überragten Condylus” (condyle surmounted by a thorn-shaped [medial] epicondyle). No additional specimens of the distal humerus of *C. prisca* were described by Sigé and Russell (1980). However, Revilliod (1917), Russell and Sigé (1970), and Sigé and Russell (1980) described the distal humerus for both *P. tupaiodon* and *P. spiegelii*. Revilliod’s (1917: fig. 9) illustration of the distal humerus of *P. spiegelii*, refigured by Russell and Sigé (1970: fig. 11), shows the distal epiphysis strongly offset laterally from the diaphysis, such that the medial edge of the trochlea is beyond the central longitudinal axis of the shaft, and the medial epicondyle is extremely wide, making up about half of the distal width of the epiphysis while the articular surfaces (trochlea and capitulum) make up the other half. In the Elderberry Canyon humerus the articular surfaces are situated more medially than in *C. prisca*, such that the medial edge of the trochlea is not beyond the central longitudinal axis of the diaphysis, and the medial epicondyle makes up about one-third of the distal width of the epiphysis while the articular surfaces make up about two-thirds.

The final bat specimen from Elderberry Canyon, USNM PAL 544094, is a jumble of crushed limb bones embedded in a

wafer of glue that obscures most parts. There appear to be much of a radius and pieces of metacarpals, as well as stray bone fragments. No measurements were made on any of these pieces.

DISCUSSION

Despite the small total number of specimens (eight; of which three are unassignable to family), the three species of bats assignable to three families from the late early or earliest middle Eocene of Elderberry Canyon, Nevada, comprise the most diverse Eocene assemblage of bats yet found in a single small quarry and single stratigraphic layer in the Western Hemisphere. In North America, older bats are well known from the Green River Formation of Wyoming and include some of the evolutionarily least derived and oldest known taxa (not including older late Paleocene, Clarkforkian, Cf3, isolated tooth fragments identified as cf. *Icaronycteris* from the Clarks Fork Basin, Willwood Formation, elsewhere in Wyoming; Gingerich, 1987; Bloch and Bowen, 2001). The Green River bats originated from the Sandwich Beds and the 18 Inch Layer in the Fossil Butte Member of the formation and include two taxa, the onychonycterid *Onychonycteris finneyi* and the icaronycterid *Icaronycteris index* from the late early Eocene (late Wasatchian, Lostcabinian, biochron Wa7; Jepsen, 1966, 1970; Simmons et al., 2008; Smith et al., 2012). A second species of *Icaronycteris* might also occur in the Bridgerian part of the Green River Formation (Jepsen, 1966; Smith et al., 2012) but is not known to be contemporaneous with other Green River Formation bats. Also in the early Eocene (late Wasatchian, Wa7) Wind River Formation of central Wyoming is the onychonycterid *Honrovits tsuwape*, the sole bat yet known in the formation (Beard et al., 1992). Other North American middle Eocene occurrences besides Elderberry Canyon are the unidentified bat from the Clarno Nut Beds (Br3) and the unidentified jaw fragment from the Bridgerian age Tabernacle Butte LF in Wyoming (McKenna et al., 1962). Another is *Wallia scalopidens* from the late Uintan (middle middle Eocene) Swift Current Creek LF in Saskatchewan, Canada (Storer, 1984). *Wallia* was originally described as a proscalopid mole but was reassessed as a molossid bat by Legendre (1985). The status of *Wallia* as a molossid was questioned by Smith et al. (2012), who instead referred it to Chiroptera incertae sedis.

Elsewhere, Eocene localities in Asia (including the Indian subcontinent), Europe, Africa, Australia, and South America have produced bat fossils or faunas of approximately the same age as the Elderberry Canyon LF. On the Eocene subcontinent of Indo-Pakistan, the Vastan Lignite Mine has yielded the most diverse Eocene bat assemblage yet known, an early Eocene, middle late Ypresian age fauna with seven species in four or five archaic families (Smith et al., 2007, 2012). Two plesiomorphic molars from the early Eocene of China represent a species of *Altaynycteris* that cannot be assigned to a known family and indicate greater early bat diversity in Paratethyan Asia than was previously recognized in other parts of the world (Jones et al., 2021).

Two bat molars from the early middle Eocene Kuldana Formation in Pakistan are as yet unidentifiable beyond Chiroptera (Russell and Gingerich, 1981). In Europe many species of bats occur in the Eocene portions of the various Quercy karstic phosphorite deposits of southern France, but most are younger than the late Ypresian–early Lutetian age of the Elderberry Canyon LF (MP 10–11 in the European mammalian biochronology; Sigé and Hugueney, 2006; Maitre, 2014). Only two Quercy localities represent MP 10, Vielase and Cazals, with no bats known from Cazals and only an indeterminate archaeonycterid from Vielase (Legendre et al., 1992), and no localities are of MP 11 age, although the exact age of some localities with bats is unknown (Sigé and Hugueney, 2006; Sigé, 2011). One such bat fossil from Quercy of unknown provenance and age, the distinctive necromantid *Cryptobune*, potentially dates to the late early Eocene or middle Eocene on the basis of its stage of evolution and plesiomorphic characters relative to those of confamilial *Necromantis*, or else it represents a later Paleogene member of the lineage (Sigé, 2011). An upper Ypresian specimen of the hassianycterid *Hassianycteris joeli* is known from Belgium (Smith and Russell, 1992), and the palaeochiropterygid *Palaeochiropteryx* cf. *tupaionodon* is known from Grauves Quarry (MP 10), France (Russell et al., 1973). More recently, an archaeonycterid, *Xylonycteris*, and a vespertilionid, *Premonycteris*, were described from Prémontre in the Paris Basin, France, of late Ypresian (MP 10) age (Hand et al., 2016; Hand and Sigé, 2018). Also notable in Europe, bats are the most abundant mammals known in the middle Eocene (MP 11) lagerstätte at Messel, Germany, with four families and four genera (*Archaeonycteris* in Archaeonycteridae, *Palaeochiropteryx* in Palaeochiropterygidae, *Hassianycteris* in Hassianycteridae, and *Tachypteron* in Emballonuridae; Russell and Sigé, 1970; Habersetzer et al., 1992, 1994; Storch et al., 2002; Morlo et al., 2004). In northern Africa, fossil bats similar in age to the Elderberry Canyon LF include, at Chambi, Tunisia (late early Eocene to early middle Eocene), ?*Necromantis* (Necromantidae), ?*Palaeophyllophora* and *Hipposideros* (Hipposideridae), *Vespertiliavus* (Emballonuridae), *Khoufechia* (Nycteridae), *Chambinycteris* (family indeterminate), *Dizzya* (Philisidae), and genus indeterminate (Vespertilionidae; Sigé, 1991; Hartenberger et al., 2001; Ravel et al., 2016) and, at Glib Zegdou, Algeria (late early Eocene to early middle Eocene), *Pseudovespertiliavus* (Emballonuridae) and *Drakonycteris* (family indeterminate; Ravel et al., 2016). Also noteworthy in eastern Africa is the tanzanycterid *Tanzanycteris*, from the middle middle Eocene, early Lutetian, from Mahenge, Tanzania (Gunnell et al., 2003; Smith et al., 2012). In Australia the archaeonycterid *Australonycteris* from the Tingamarra LF, Queensland, is associated with a radiometric age of 54.6 Ma (Hand et al., 1994) and thus is older than the Elderberry Canyon LF. One of the few known occurrences of a Paleogene chiropteran in South America is that of a species of indeterminate systematic relationships from Laguna Fría, Chubut, Argentina, represented by only two partial lower molars (Tejedor et al., 2005). The diverse fauna of mammals from Laguna Fría combined with other nearby localities provides the

Paso del Sapo fauna, which was tentatively established as a new South American Land Mammal Age, the “Sapoan” SALMA. The Paso del Sapo fauna was considered by Tejedor et al. (2009) to reflect the late early Eocene, but more recent work puts it slightly younger, in the early middle Eocene, associated with radiometric dates of 49–47 Ma (Woodburne et al., 2014), whereas the Laguna Fría fauna itself is delimited by dates for underlying and overlying basalts of 49 and 43 Ma, respectively (Gosses et al., 2021), making the Laguna Fría fauna approximately coeval with the Br1b–Br2 Elderberry Canyon LF. Additional finds of Paleogene bats in South America and potentially Antarctica (the La Meseta fauna of the Antarctic Peninsula is essentially contemporaneous with the Paso del Sapo fauna and is included in the “Sapoan” SALMA; Goin et al., 2016) are eagerly awaited and will, of course, be significant in establishing the global biogeographic relationships of early bats.

The occurrence of *Palaeochiropteryx sambuceus* in the Elderberry Canyon LF provides the first occurrence of the genus *Palaeochiropteryx* and of the family Palaeochiropterygidae outside of Europe. As noted above, *Palaeochiropteryx* species were previously known only in Europe, primarily in the Messel Quarry in Germany, where they are by far the commonest fossil bats in the Messel paleofauna (Morlo et al., 2004). The temporal record of the genus *Palaeochiropteryx* in Europe ranges from late early Eocene (MP 10; late/upper Ypresian) in the Grauves Quarry, Paris Basin, France (Russell et al., 1973), to early middle Eocene (MP 11; early/lower Lutetian) at Messel (Smith et al., 2012), contemporaneous with the Elderberry Canyon LF and *P. sambuceus* in North America. The establishment of *Volactrix simmonsae* as a possible onychonycterid potentially increases the North American diversity of that family to three genera. And the referral of the new taxon *Sonor handae* to Vespertilionidae provides the earliest occurrence of the family in North America, slightly younger than the early Eocene *Premonycteris vesper* from Europe and the early middle Eocene indeterminate vespertilionid from North Africa (Hand et al., 2016; Ravel et al., 2016). As noted above, *Sonor handae* is rather similar in some characteristics to the vespertilionid subfamily Kerivoulinae. Horáček (1988) and Čermák et al. (2007) provided the only pre-Quaternary fossil records of a kerivoulinae in the Pliocene (near the MN 16/17 boundary and near the MN 15b/16a boundary, respectively) in the Czech Republic, far outside the modern Afrotropical–Indomalayan–Australasian range of the subfamily. *Sonor handae* possibly represents a much earlier member of the kerivoulinae lineage and a geographic extension of its range into North America or an unrelated early bat having certain osteodontal features convergently evolved with those of kerivoulines. Definitive conclusions about its affinities cannot be made without more complete material.

Whereas early early Eocene localities around the world include only archaic bat families, the Elderberry Canyon bat fauna resembles other late early to middle Eocene faunas in having a combination of archaic (?Onychonycteridae and Palaeochiropterygidae) and modern (Vespertilionidae) families (Smith et al., 2012; Hand et al., 2015). Global paleoclimatic warming during

the PETM (ca. 56 Ma) and EECO (spanning approximately 54–47 Ma; Tsukui and Clyde, 2012; Westerhold et al., 2020) established the highest warming periods of the Cenozoic, including in the High Arctic (Cramwinckel et al., 2018; Westerhold et al., 2020). The warming from at least the Paleocene–Eocene boundary and during the early Eocene probably facilitated range shifts into high latitudes and intercontinental dispersals for bats, as it did for other vertebrates across Asia–Europe–Greenland–North America landmasses (e.g., West and Dawson, 1978; McKenna, 1980; Beard and Dawson, 1999; Eberle and McKenna, 2002; Hooker and Dashzeveg, 2003; Smith et al., 2006; Aubry et al., 2007; Dawson, 2012; Eberle and Greenwood, 2012; Eberle and Eberth, 2015; Hooker, 2015; Stidham and Eberle, 2016; Kay, 2018). The Elderberry Canyon LF represents a later period, ~50–47 Ma, near the end of the EECO during which there were few mammalian dispersals to North America (Woodburne, 2004). The Bridgerian NALMA represents the early stages of a long cooling trend after the EECO peak that caused great faunal turnover (Blois and Hadly, 2009; Woodburne et al., 2009a, 2009b), even though global average temperatures remained near 26°C in the early middle Eocene (Cramwinckel et al., 2018). Importantly, Woodburne et al. (2009a, 2009b) argued that although conditions apparently stimulated intercontinental and intracontinental migrations of plants and land mammals during the PETM, the EECO saw intercontinental migrations that were initially stymied and early autochthonous mammalian diversification that was enhanced but then precipitously began dropping later in the EECO. The EECO alongside relatively warm but declining global temperatures may have contributed to the change in north temperate bat faunas from archaic families to modern groups (Smith et al., 2012), potentially favoring those bats capable of thermoregulation strategies, enabling their survival at cooling medium and higher latitudes (Yu et al., 2014). Undoubtedly, other abiotic and biotic selection factors acted on them as well. Intercontinental corridors among the northern landmasses reflect the connectivity indicated by the late early Eocene–early middle Eocene presence of *Palaeochiropteryx* in North America and Europe. The tectonically active Nevadaplano and surrounding regions of western North America, together with concordant climate and ecological changes (Woodburne et al., 2009a, 2009b), must have strongly influenced the evolution of Eocene mammals in the western interior of the continent, although the influence of these processes on the Elderberry Canyon bats cannot be directly investigated. Tectonic processes and topographic complexity

greatly affected mammalian diversification and biogeography in tectonically active regions of North America throughout the Paleogene (and increasing in the Neogene; Badgley, 2010; Loughney et al., 2021). Geological evidence suggests that the Sheep Pass Formation represents a long-duration, probably high elevation graben lake and wetland system created by extensional tectonics rather than Laramide orogeny like what was occurring farther to the east (Good, 1987; DeCelles, 2004; Druschke et al., 2011; Chamberlain et al., 2012; Bonde et al., 2020). This lake and wetland system would have provided much of the habitat utilized by the Elderberry Canyon bats.

ACKNOWLEDGMENTS

Fossils were discovered at Elderberry Canyon by Thomas D. Fouch, Melissa Fouch, and Forrest G. Poole of the U.S. Geological Survey in 1975 and were subsequently collected using a jackhammer, sledgehammer, and other tools and hand carried down the mountain by author RJE with the able assistance of Fouch, Dan Chaney, Fred Grady, John Flynn, Arnold Lewis, and Michael Pechacek. They were expertly and meticulously prepared from the limestone matrix using dilute formic acid by Fred Grady and Dan Chaney. The loan of specimens was made possible by Michael Brett-Surman, Mark S. Florence, Jennifer Strotman, Amanda Millhouse, and Jessica K. Nakano of the USNM. Jennifer Larsen helped with loans received at the Oklahoma Museum of Natural History. The partial skeleton was scanned at MICRO, for which we also acknowledge the Oklahoma State University Center for Health Sciences, University of Arkansas, Fayetteville, and the National Science Foundation (NSF grant 1725925 to authors HDO and PMG). Holly Little, USNM PAL, graciously aided in providing helpful advice and ARKs for digital representations of *P. sam-buceus*. The late Donald E. Savage of the University of California Museum of Paleontology provided casts of European Eocene bats that were invaluable for comparisons. Steve Westrop and Roger Burkhalter of the Oklahoma Museum of Natural History kindly allowed the use of their bellows camera and focus-stacking hardware and software for the photography of many specimens. We deeply appreciate the time and efforts of all these people, as well as the two anonymous reviewers, whose work and insights substantially enhanced the manuscript. Photo and image credits are as follows: Figures 1–3, 6, 9–11 by N. J. Czaplewski; Figures 4, 5, 7 by Paul M. Gignac; and Figure 8 by Haley D. O'Brien.

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