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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"

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ABSTRACT

A new fossil from the Late Eocene BQ-2 locality in the Birket Qarun Formation in the Fayum Depression of northern Egypt (dated to ~37 mybp) does not fit within the diagnosis of any previously described family of bats from Africa or any other continent. Known from a partial maxilla, this taxon has dilambdodont tribosphenic molars with a well-developed, symmetrical, W-shaped ectoloph lacking a distinct mesostyle but with a strong parastyle and shallow U-shaped ectoflexus—all traits that are found in most archaic bat families and that are probably plesiomorphic for bats. However, this taxon also has an M2 with a large metaconule cusp and a large, bulbous hypocone set low on the posterolingual corner of the tooth, neither of which occur in any known bat family, living or extinct. Also notable is the size of the new BQ-2 bat, which appears to have been approximately the same size as the largest extant bats with dilambdodont dentitions, falling well within the size range of plant-eating megabats and carnivorous bats from several extant lineages. The combination of traits in the new BQ-2 bat suggests that it was omnivorous, probably including insects, small vertebrates, and plant material its diet. In this regard it represents an ecological niche previously unknown among archaic Eocene bats, which are otherwise thought to have been strictly animalivorous. Because extinct Eocene bat families exhibit considerable mosaic evolution in morphological traits, do not seem to have inhabited a uniform ecological niche, and do not form a monophyletic group, we argue against use of the name "Eochiroptera" to collectively refer to these taxa.

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INTRODUCTION

The Eocene was a time of explosive diversification for Chiroptera. The oldest-known bats are early Eocene in age (~55–52 mybp) and bats were present on nearly every continent by the late Eocene (~34 mybp; Gunnell and Simmons, 2005; Tabuce et al., 2009; Smith et al., 2007, 2012; Hand et al., 2015). Thirty families of bats are currently recognized, including 10 families known only from fossils (table 1). A combination of fossil evidence and ghost-lineage reconstruction indicates that virtually all of these lineages were distinct by the end of the Eocene (Teeling et al., 2005, 2012; Simmons, 2005a; Miller-Butterworth et al., 2007; Agnarsson et al., 2011; Meredith et al., 2012). Well-preserved skeletons of many taxa (e.g., *Onychonycteris, Icaronycteris, Archaeonycteris, Palaeochiropteryx, Hassianycteris*) indicate that the earliest bats were capable of powered flapping flight, and all but *Onychonycteris* probably used laryngeal echolocation (Novacek, 1985, 1987; Habersetzer and Storch, 1989; Simmons and Geisler, 1998; Simmons et al., 2008, 2010). Powered flight and laryngeal echolocation—both clearly adaptive traits—are widely thought to have been key features that enabled rapid diversification and spread of bats across the globe in the Eocene (e.g., Novacek, 1985; Sigé, 1985, 1991; Simmons, 2005a; Teeling et al., 2005; Gunnell and Simmons, 2005).

The oldest-known African bat fossils come from El Kohol in Algeria and are early Eocene in age (~54-52 mybp, Ypresian; Ravel et al., 2011). Unfortunately, the El Kohol bats are too fragmentary to identify beyond recognizing that they are clearly bats (Ravel et al., 2011). In Africa, 15 families of bats are presently known (table 1) and most of these have fossil records that extend back at least into the early Oligocene or late Eocene (Sigé, 1985, 1991; Gunnell and Simmons, 2005; Gunnell et al., 2008, 2014; Ravel et al., 2011, 2015). The majority of Paleogene bat fossils from the African region come from North African localities including Chambi (Tunisia, late early Eocene) and the Fayum Depression (Egypt, late Eocene to early Oligocene; Sigé, 1985, 1991; Gunnell and Simmons, 2005; Gunnell et al., 2008 Ravel et al., 2011, 2015). Isolated teeth are also known from the Arabian Peninsula (Taqah, Sultanate of Oman, early Oligocene), which was contiguous with Africa during the later Paleogene (Sigé et al., 1994).

The Fayum Depression in Egypt (fig. 1) has been known as a source of abundant Paleogene fossil mammals since the late 1800s when collectors first began working in the region. Early anthropoid primates, hyracoids, rodents, proboscideans, macroscelideans, tenrecoids, hyaenodontids, embrithopods, and other mammals have emerged from Fayum deposits over many decades of field exploration (Dames, 1894; Andrews, 1901, 1906; Andrews and Beadnell, 1902; Osborn, 1908, 1909; Schlosser, 1910, 1911; Wood, 1968; Simons and Gingerich, 1974, 1976; Simons and Kay, 1983; Simons, 1989, 1992, 1995; Simons et al., 1991; Simons and Bown, 1995; Seiffert et al., 2003, 2005, 2008, 2009, 2010; Boyer et al., 2010; Sallam et al., 2010a, 2010b, 2011). While relatively rare, in recent years bats from the Fayum have proven to be both diverse and biogeographically significant (Sigé, 1985; Gunnell et al., 2008, 2014). Ten bat species representing six families have been described previously from Fayum deposits, including the oldest-known rhinopomatids, megadermatids, and myzopodids (table 2). Four Fayum bat species represent an extinct

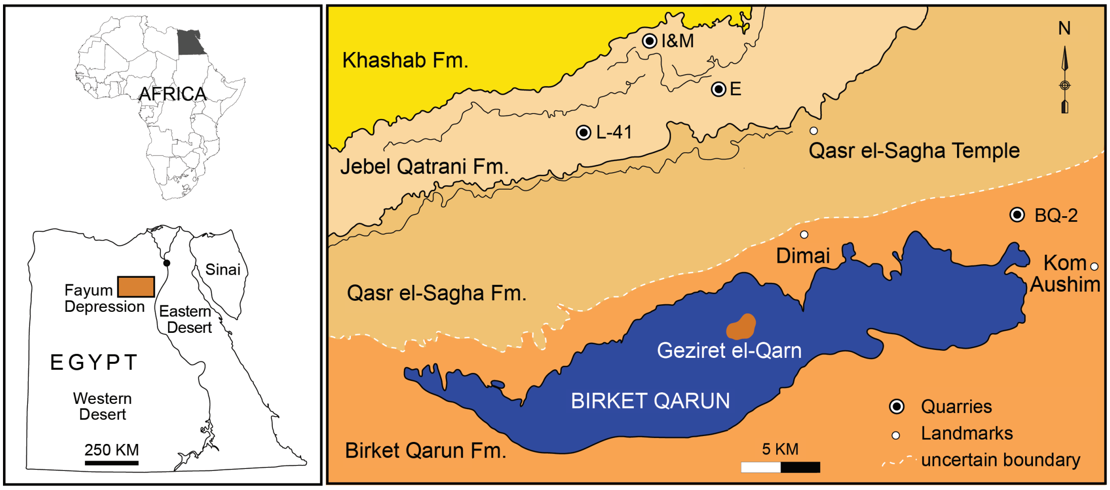

FIGURE 1. Maps showing the location of the Fayum Depression in Egypt (left and the geographic position of the BQ-2 Quarry (right) within the Birket Qarun Formation (modified from Sallam et al., 2011).

family (Philisidae), but the remainder of the fossil bats reported to date belong to extant families (Sigé, 1985; Gunnell et al., 2008, 2014).

Several localities of different ages in the Fayum Depression have produced bat fossils (table 2; fig. 2). These include two Eocene quarry sites (L-41 and BQ-2) and one Oligocene locality (Quarry I; Sigé, 1985; Gunnell et al., 2008, 2014). Quarry I, which has produced philisids and myzopodids, is now thought to be early Oligocene (Rupelian), dating to ~30 Ma. (Sigé, 1985; Seiffert, 2006; Gunnell et al., 2008, 2014; Ravel et al., 2011). Slightly older is L-41, which has produced emballonurids, megadermatids, and vespertilionids (Gunnell et al., 2008). L-41 is now thought to be late Eocene (Priabonian) in age, ~ 34 Ma (Gunnell et al., 2008; Seiffert, 2006, 2010; Ravel et al., 2011). BQ-2, which has produced philisids, rhinopomatids, and myzopodids, and a possible bat or marsupial (*Ghamidtherium*) is also thought to be Priabonian but is somewhat older, dating to ~37 Ma (Sánchez-Villagra et al., 2007; Gunnell et al. 2008, 2014; Seiffert, 2006, 2010; Ravel et al., 2011).

The mammal fossils from BQ-2 (Birket Qarun Locality 2) are found in the Umm Rigl Member of the Birket Qarun Formation (Seiffert et al., 2008). The fossil-bearing layers at BQ-2 are fluvial in origin and ironstone rich, composed of fining-upward sequences of medium- to fine-grained mud and sandstones, presumably deposited by meandering streams that occasionally became ponded and stagnant (Seiffert et al., 2008). The presence of nearshore marine layers both above and below the BQ-2 mammal-bearing layers suggests that the BQ-2 deposits were deposited very close to the coast (Seiffert et al., 2008), but the ichthyofauna that is associated with the fossil described here includes freshwater fishes, attesting to the terrestrial riverine nature of the deposit (Murray et al., 2010). Abundant, fairly complete, unabraded jaws and postcranial bones of arboreal primates are also found in the same deposit, suggesting that the area around BQ-2 was densely forested (Seiffert et al., 2003, 2005, 2008, 2009, 2010; Boyer et al., 2010).

TABLE 1. Currently recognized extant (regular type) and extinct (bold type) bat families: X = extant; F = fossil only. Regions: NA = North America; C = Caribbean; SA = South America; E = Europe; A = Africa; M = Madagascar; IP = Indo-Pakistan; MA = Mainland Asia; OA = Oceanic Asia; Au = Australia; NZ = New Zealand.

Family	NA	C	SA	E	A	M	IP	MA	OA	Au	NZ	References & Notes
Onychonycteridae	F			F								Simmons et al., 2008; Smith et al., 2012
Icaronycteridae	F			F			F					Jepsen, 1966; Smith et al., 2012
Archaeonycteridae				F			F					Revilliod, 1917; Smith et al., 2012
Hassianycteridae				F			F					Habersetzer and Storch, 1987; Smith et al., 2012
Palaeochiropterygidae				F			F	F				Revilliod, 1917; Smith et al. 2012
Aegyptonycteridae					F							This paper
Philisidae					F							Sigé, 1985; Gunnell et al., 2008; Smith et al., 2012
Tanzanycteridae					F							Gunnell et al., 2003
Mixopterygidae				F								Maitre et al., 2008; Smith et al., 2012
Necromantidae				F	F							Sigé, 2011a
Speonycteridae	F											Czaplewski and Morgan, 2012
Pteropodidae				F	X	X	X	X	X	X		Gray, 1821; Aguilar et al., 1986; Qui et al., 1985; Ducrocq et al., 1993; Simmons, 2005b; Gunnell, 2010
Rhinolophidae				X	X		X	X	X	X		Gray, 1825; Simmons, 2005b
Hipposideridae				F	X	X	X	X	X	X		Flower and Lydekker, 1891; McKenna and Bell, 1997; Simmons, 2005b
Rhinonycteridae				F	X	X		X		X		Gray, 1866a; Foley et al., 2014
Megadermatidae					X		X	X	X	X		Allen, 1864; Simmons, 2005b
Rhinopomatidae				F	X		X	X	X			Bonaparte, 1838; Simmons, 2005b; Hulva et al., 2007
Craseonycteridae								X				Hill, 1974; Simmons, 2005b
Emballonuridae	X		X	F	X	X	X	X	X	X		Gervais, 1855; Storch et al., 2002; Simmons, 2005b
Nycteridae				F	X	X		X	X			Van der Hoeven, 1855; Simmons, 2005b; Sigé, 2011b

Family	NA	C	SA	E	A	M	IP	MA	OA	Au	NZ	References & Notes
Myzopodidae					F	X						Thomas, 1904; Simmons, 2005b; Gunnell et al., 2014
Mystacinidae										F	X	Dobson, 1875; Hand et al., 1998, 2005; Simmons, 2005b
Phyllostomidae	X	X	X									Gray, 1825; Simmons, 2005b
Mormoopidae	X	X	X									Saussure, 1860; Simmons, 2005b
Noctilionidae	X	X	X									Gray, 1821; Simmons, 2005b
Furipteridae	X		X									Gray, 1866; Simmons, 2005b
Thyropteridae	X		X									Miller, 1907; Simmons, 2005b
Natalidae	X	X	X									Gray, 1866b; Simmons, 2005b
Molossidae	X	X	X	X	X	X	X	X	X	X		Gervais, 1856; Simmons, 2005b
Vespertilionidae	X	X	X	X	X	X	X	X	X	X		Gray, 1821; Simmons, 2005b
Miniopteridae				X	X	X	X	X	X	X		Dobson, 1875; Simmons, 2005; Miller-Butterworth et al., 2007
Cistugidae					X							Simmons, 2005b; Lack et al., 2010

In 2006 excavations at BQ-2 resulted in discovery of a maxilla fragment with two teeth that appears to be a fossil bat but one that does not fit within the diagnosis of any previously described family of bats from Africa or any other continent. This specimen is herein described as representing a new bat family and its significance is discussed below.

METHODS

Excavation: Locality BQ-2 has been excavated by careful quarrying with brushes and ice-picks, followed by dry screening. The fossils tend to be closely associated with authigenic limonite, which is removed piece by piece; larger fossils that are discovered are consolidated in place with polyvinyl acetate and extracted for further preparation, and all sediment from the site is subsequently screened for smaller fossils. The latter work often leads to the recovery of isolated teeth, such as those of *Qarunycteris* and *Witwatia* that were described by Gunnell et al. (2008). The specimen described here was consolidated in the field and prepared at Stony Brook University.

Measurements: Where possible, tooth measurements of extant and extinct bats were made with a reticle micrometer mounted in a binocular microscope eyepiece and calibrated

TABLE 2. Bats described from the Birket Qarun and Jebel Qatrani formations in the Fayum.

Family	Genus	Species	Locality	Age	Primary Reference
Aegyptonycteridae	*Aegyptonycteris*	*knightae*	BQ-2 Quarry	Priabonian (37 Ma)	This paper
Philisidae	*Philisis*	*sphingis*	Quarry I	Rupelian (30 Ma)	Sigé, 1985
	Witwatia	*schlosseri*	BQ-2 Quarry	Priabonian (37 Ma)	Gunnell et al., 2008
	Witwatia	*eremicus*	BQ-2 Quarry	Priabonian (37 Ma)	Gunnell et al., 2008
Emballonuridae	*Dhofarella*	*sigei*	Quarry L-41	Priabonian (34 Ma)	Gunnell et al., 2008
Rhinopomatidae	*Qarunycteris*	*moerisae*	BQ-2 Quarry	Priabonian (37 Ma)	Gunnell et al., 2008
Megadermatidae	*Saharaderma*	*pseudovampyrus*	Quarry L-41	Priabonian (34 Ma)	Gunnell et al., 2008
Vespertilionidae	*Khonsunycteris*	*aegypticus*	Quarry L-41	Priabonian (34 Ma)	Gunnell et al., 2008
Myzopodidae	*Phasmatonycteris*	*phiomensis*	Quarry I	Rupelian (30 Ma)	Gunnell et al., 2014
	Phasmatonycteris	*butleri*	BQ-2 Quarry	Priabonian (37 Ma)	Gunnell et al., 2014
Family uncertain	*Vampyravus*	*orientalis*	Upper Sequence?	Rupelian?	Schlosser, 1910, 1911

using a stage micrometer. Measurements were recorded to the nearest tenth of a millimeter. In the case of fossil bat skeletons with teeth preserved in occlusion, tooth measurements were calculated from scaled X rays, digital photographs, or digital renderings of micro-CT images.

Dental Comparisons: The molar teeth of the new fossil were compared with specimens, casts, CT images, and literature descriptions of teeth of bats and other mammals known to have dilambdodont molars (see appendix 1 and citations below). Comparisons with many species of noctilionoid bats were made using the illustrated data matrix of dental characters published by Dávalos et al. (2014) and made available online in MorphoBank (www.morphobank.org) as project P891. MorphoBank is a public online database for assembling and managing morphological matrices (O'Leary and Kaufman, 2012). Each cell in the matrix is documented with a labeled image that can be zoomed into or downloaded to better observe the structure in question. Morphological observations based on specimens published in MorphoBank project P891 are attributed to "Dávalos et al. (2014: P891)" in the discussion below.

Institutional Abbreviations: **AMNH,** American Museum of Natural History, New York, New York; **CGM,** Cairo Geological Museum, Cairo, Egypt; **FMNH,** Field Museum of Natural History, Chicago, Illinois; **RBINS,** Royal Belgian Institute of Natural Sciences, Brussels, Belgium; **ROM**, Royal Ontario Museum, Toronto, Canada; **SMF**, Forschungsinstitut Senckenberg, Mammalogy, Frankurt am Main, Germany; **UMMZ,** University of Michigan Museum of Zoology, Ann Arbor, Michigan; **YPM,** Yale Peabody Museum, New Haven, Connecticut.

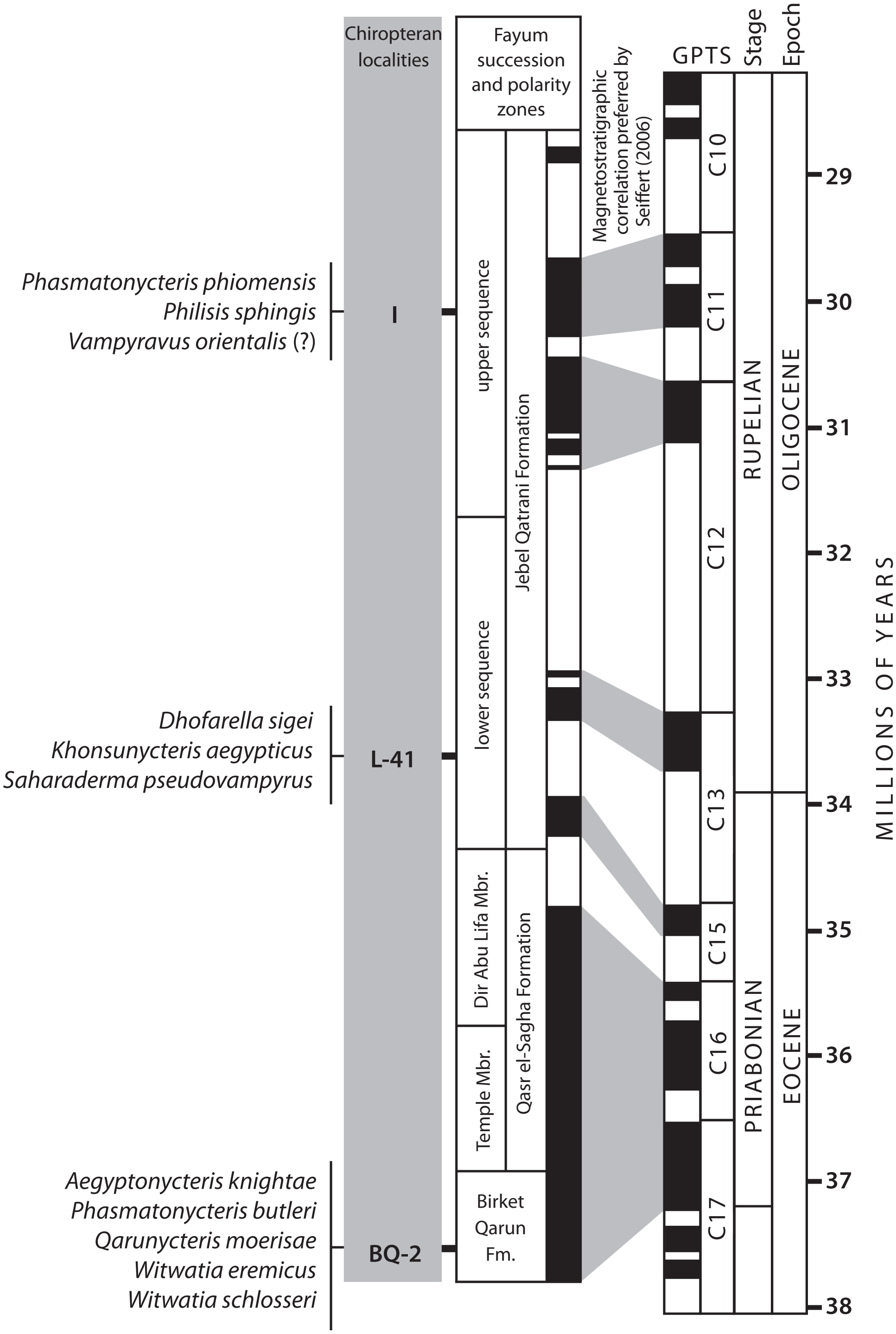

FIGURE 2. Fayum stratigraphic sequence and the distribution of bat taxa from quarries BQ-2, L-41, and I.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

CHIROPTERA Blumenbach, 1779

AEGYPTONYCTERIDAE, new family

Aegyptonycteris, new genus

Aegyptonycteris knightae, new species

Figures 3–5

Holotype: CGM 83740, fragment of right maxilla with M2 and M3; only known specimen.

Locality and Horizon: Fayum Quarry BQ-2, 23 meter level, Birket Qarun Formation, Fayum Depression, Western Desert, Egypt (Fig. 1-2).

Age: Late Eocene, Priabonian, ~37 Ma.

Etymology: From *Aegyptus*, Latinized Greek for "Egypt," and *nycteris*, Greek for "bat." The genus name refers to the country in which this new taxon was discovered. The specific epithet is given in honor of Mary Knight, Managing Editor of the American Museum of Natural History Scientific Publications, in recognition of the enormous contributions she has made to dissemination of the results of scientific research over the years, as well as her lifelong devotion to the people and culture of Egypt.

Diagnosis: A large bat with dilambdodont tribosphenic upper molars that have a well-developed W-shaped ectoloph and strong, curved parastyle; neomorphic cusp (ectostyle) present between parastyle and centrocrista; mesostyle absent; protocone well developed; large metaconule present; paraconule absent but small crest (paraloph) present between protocone and base of paracone; preprotocrista continuous with precingulum; postprotocrista runs roughly parallel to long axis of tooth row, connects protocone with metaconule; trigon (protofossa) narrow and enclosed labially by a complete centrocrista; lingual and labial cingulae absent but precingulum present; M3 only slightly smaller than M2 in buccolingual width; M2 subrectangular with a wide precingulum, shallow U-shaped ectoflexus, curved metastyle, and a large, bulbous hypocone set low on the posterolingual corner of the tooth; M3 with a well-developed protocone, paracone, and metacone, narrow precingulum, and rounded hypocone shelf; postmetacrista and metastyle absent but tooth not mesiodistally compressed.

Description and Comparisons: *Aegyptonycteris knightae* is a large bat by any measure. The dimensions of its teeth are comparable to those of the largest living echolocating bats as well as of the largest-known extinct taxa (table 3; fig. 6). Among previously described bats with dilambdodont dentitions, the largest-known taxa include phyllostomids (e.g., *Vampyrum*, *Chrotopterus*, *Phyllostomus*), molossids (e.g., *Cheiromeles*, *Eumops*), megadermatids (e.g., *Macroderma*), the enigmatic Eocene taxon *Necromantis adichaster*, and members of the extinct family Philisidae including *Witwatia schlosseri* from the Fayum and *W. sigei* from Tunisia and Algeria (Gunnell et al., 2008; Hand et al., 2012; Giannini et al., 2012; Ravel et al., 2015). The

TABLE 3. Measurements of M2 and M3 in selected large bats with tribosphenic dentitions; extinct species are shown in bold. L = length, W = width, and * indicates species mean based on two or more specimens. Mean body mass is provided for extant species (based on 10 specimens where available). Measurements taken by G.F.G. based on collections at the University of Michigan, Museum of Zoology (Ann Arbor), the American Museum of Natural History (New York), the Museum National d'Histoire Naturelle (Paris), the Royal Belgian Institute of Natural Sciences (Brussels), the Senckenberg Forschungsinstitut (Frankfurt), and in some cases from the literature (Gunnell et al., 2008, for *Witwatia schlosseri*; Ravel et al., 2012, for *Witwatia sigei*; Hand et al., 1988, for *Macroderma koppa*).

Family	Genus	Species	M2L	M2W	M3L	M3W	Mass (g)
Phyllostomidae	*Vampyrum*	*spectrum*	3.84	4.84	–	–	169.4
Megadermatidae	*Macroderma*	*gigas*	3.27	3.54	1.81	3.38	126.4
Molossidae	*Eumops*	*dabbenei**	3.20	3.45	1.70	3.00	104.4
Emballonuridae	*Saccolaimus*	*peli*	3.39	3.81	1.12	3.02	100.0
Hipposideridae	*Hipposideros*	*commersoni*	3.07	4.03	1.50	2.94	99.1
Phyllostomidae	*Phyllostomus*	*hastatus*	3.10	3.50	1.20	3.30	92.5
Phyllostomidae	*Artibeus*	*fimbriatus**	3.06	3.68	2.48	3.38	63.9
Molossidae	*Eumops*	*perotis*	3.30	3.70	1.60	2.90	51.1
Megadermatidae	*Megaderma*	*lyra*	2.79	3.26	1.29	3.00	45.5
Emballonuridae	*Taphozous*	*nudiventris**	2.69	3.23	0.96	2.75	34.1
Vespertilionidae	*Myotis*	*myotis**	2.15	2.75	1.05	2.60	24.8
Vespertilionidae	*Hesperopterus*	*tickelli*	2.20	2.80	1.30	2.10	16.3
Aegyptonycteridae	***Aegyptonycteris***	***knightae***	**4.03**	**4.83**	**2.67**	**4.42**	–
Philisidae	***Witwatia***	***schlosseri****	**4.00**	**5.52**	–	–	–
Philisidae	***Witwatia***	***schlosseri***	–	–	**3.70**	**4.20**	–
Philisidae	***Witwatia***	***sigei***	**3.80**	**4.30**	–	–	–
Necromantidae	***Necromantis***	***adichaster***	**3.30**	**4.29**	–	–	–
Megadermatidae	***Macroderma***	***koppa****	**3.85**	**4.55**	**1.95**	**4.40**	–

upper molars of *Aegyptonycteris* are larger than those of all known tribosphenic bats with the exception of *Witwatia schlosseri,* which has a slightly larger M2 (fig. 6). The M3 in *Aegyptonycteris* is shorter but slightly broader than that of *Witwatia schlosseri* (table 3; fig. 6).

The holotype of *A. knightae* is a maxillary fragment that preserves the posterior portion of the orbital floor and the anterior base of the zygomatic arch (figs. 3, 4). The maxilla is broken dorsally and anteriorly making it impossible to delimit the position and extent of the optic foramen. The anterior orbital floor is relatively broad, long, and flattened with a smooth posterior surface that grades laterally into the base of the zygomatic arch. Like in most bats, the medial roots of the posterior molars can be seen breaching the surface of the orbital floor.

The molars of *Aegyptonycteris* have a well-developed W-shaped ectoloph like most other bats. The four primary cristae (preparacrista, postparacrista, premetacrista, and postmetacrista) on M2 are worn but appear to have been roughly subequal in length, with the postmetacrista only slightly longer than the preparacrista, and the two crests that form the centrocrista only slightly shorter than the preparacrista. These proportions are similar to those seen in most Eocene bats, with the

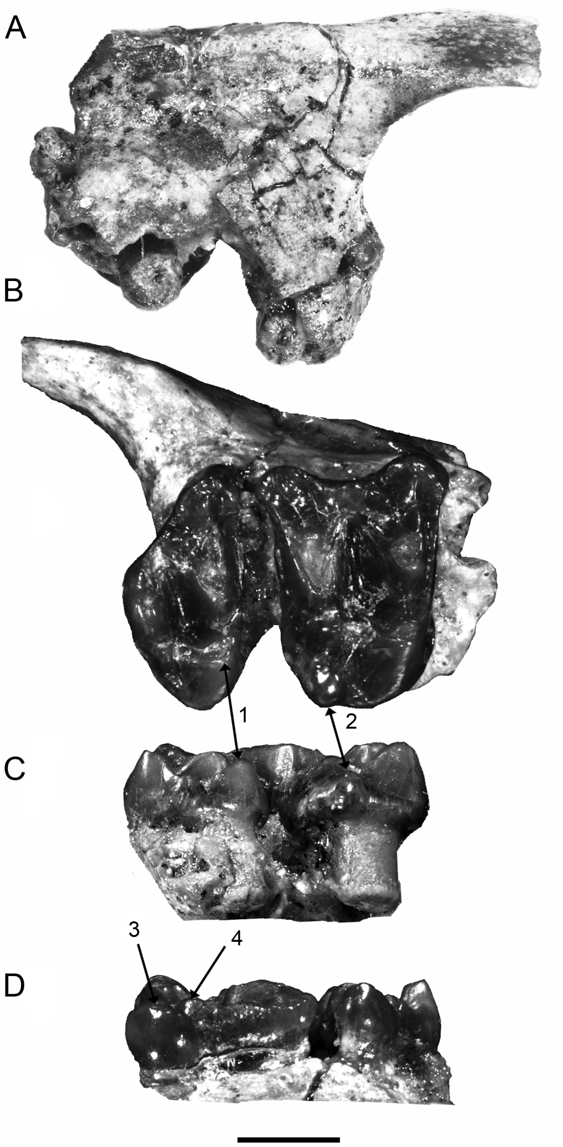

FIGURE 3. Photographs of the holotype of *Aegyptonycteris knightae* (CGM 83740): **A,** dorsal view of maxillary fragment containing M2–M3; **B,** occlusal view; **C,** lingual view; **D,** labial view. Arrows indicate: **1,** M3 protocone in occlusal and lingual views; **2,** M2 hypocone in occlusal and lingual views; **3,** M2 parastyle in labial view; **4,** neomorphic ecytostylar cusp in labial view. Scale bar = 2 mm.

exception of philisids, which do not have a complete centrocrista (Gunnell et al., 2008; Ravel et al., 2012, 2015; Smith et al., 2012). The relative height and sharpness of the primary cusps is difficult to determine due to wear, but proportions and angles of unworn portions of the crown and cristae suggest that the cusps were not notably tall or acute, nor were the cristae sharply bladelike. In this respect *Aegyptonycteris* differs from many other Paleogene bats that have tall molar cusps with more sharply defined cristae (e.g., *Icaronycteris*; Smith et al., 2012). Wear precludes determination of the original relative height of the paracone and metacone in *Aegyptonycteris*, but in their worn state they are subequal. The crowns of both M2 and M3 are relatively long (mesiodistally) compared to their width (buccolingually) and lack a well-defined waist, giving them a boxy appearance. In this *Aegyptonycteris* differs from most other Eocene bats that have molars that either are more triangular in outline (e.g., *Archaeonycteris trigonodon*) or have a distinct waist (e.g., *Archaeonycteris brailloni*, *Icaronycteris index*, *Mixopteryx dubai*, *Necromantis adichaster*) and which are proportionally somewhat shorter mesiodistally and broader buccolingually (Maitre et al., 2008; Hand et al., 2012; Smith et al., 2012). Upper molars that are rectangular or boxy in outline are found among Eocene bats only in philisids (Gunnell et al., 2008; Ravel et al., 2012). M3 in *Aegyptonycteris* is only slightly smaller than M2 in buccolingual width, a condition shared with most other Eocene bats (Smith et al., 2012).

The protocone in *Aegyptonycteris* is well developed on both M2 and M3. It is not centrally located but is instead positioned near the anterior edge of the tooth, lingual to the paracone. This resembles the condition seen in most Eocene bats (Russell and Sigé, 1970; Russell et al., 1973; Gunnell et al., 2008; Ravel et al., 2012; Hand et al., 2012; Smith et al., 2012).

FIGURE 4. Photograph of the holotype of *Aegyptonycteris knightae* (CGM 83740) in occlusal view. Scale = 4 mm.

A large metaconule is present on both molars in *Aegyptonycteris*. Very small metaconules are present in some onychonycterids (e.g., some specimens of *Ageina*), icaronycterids (e.g., *Icaronycteris index*), and some palaeochiropterygids (e.g., *Palaeochiropteryx*; Russell and Sigé, 1970; Smith et al., 2012). However, most bats lack conules entirely (Gunnell et al., 2011; Hand et al., 2012; Smith et al., 2012; Ravel et al., 2012; Dávalos et al., 2014). The presence of a large metaconule on the upper molars in *Aegyptonycteris* is a condition unique among bats.

The postprotocrista runs between the protocone and the metaconule on both molars in *Aegyptonycteris*. This resembles the condition seen in other Eocene bats that have a metaconule (e.g., *Icaronycteris index*; Smith et al., 2012). In most other bats, which lack a metaconule, the postprotocrista runs either from the protocone to the base of the metacone (e.g., *Archaeonycteris trigonodon, Necromantis*) or from the protocone to the postcingulum (e.g., mixopterygids), or from the protocone to the point where the postcingulum and lingual cingulum converge (e.g., *Witwatia sigei*; Maitre et al., 2008; Gunnell et al., 2011; Ravel et al., 2012; Hand et al., 2012; Smith et al., 2012). The postprotocrista on both molars in *Aegyptonycteris* is directed across the tooth at a shallow angle, so that it runs nearly parallel to the long axis of the toothrow. This differs from the condition seen in most Eocene bats, in which the postprotocrista is directed more obliquely, so that it runs from anterolingual to posterolabial across the tooth at a sharp angle to the longitudinal axis of the toothrow (Gunnell et al., 2011; Hand et al., 2012; Smith et al., 2012). A postprotocrista that runs roughly parallel to the long axis of the toothrow is seen among Eocene bats in *Lapichiropteryx* (a possible palaeochiropterygid from China), some spe-

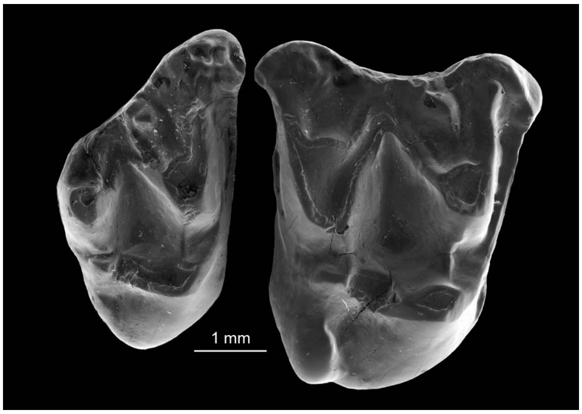

FIGURE 5. Scanning electron micrograph (in occlusal view) of the holotype of *Aegyptonycteris knightae* (CGM 83740, right maxillary fragment with M2–M3).

cies of *Mixopteryx*, some species of *Witwatia* (a philisid), and *Tachypteron* (an Eocene emballonurid; Maitre et al., 2008; Ravel et al., 2012; Smith et al., 2012).

Two crests run anterolabially from the protocone in *Aegyptonycteris*. One, the preprotocrista, runs anterolabially and is continuous with the precingulum. A second, lower crest, which we consider best described as a paraloph sensu Czaplewski et al. (2008), runs labially distal to the preprotocrista to the base of the paracone. The paraloph is definitely not cusplike in *Aegyptonycteris*, so we do not consider it to be a paraconule although it is located in a similar position. A paraloph is absent in most Eocene bats but is present in some icaronycterids, some archaeonycterids (e.g., *Archaeonycteris brailloni*), and *Dizzya*, a philisid (Hand et al., 2012; Smith et al., 2012; Ravel et al., 2015). The paraloph in the holotype of *Icaronycteris index* (YPM PU-18150) runs from the tiny paraconule to the base of the paracone rather than originating on the protocone as it does in the other taxa, raising questions about the homology of these crests.

The paracone and metacone are located near the middle of the tooth crown and the stylar shelf is well developed in *Aegyptonycteris*. The centrocrista is closed and does not reach the labial margin of the tooth on either molar, a condition also seen in onychonycterids, archaeonycterids, and hipposiderids such as *Palaeophyllophora* (Gunnell et al., 2011; Hand et al., 2012; Smith et al., 2012). However, the molars lack a distinct labial cingulum with a raised edge such as is seen in onychonycterids (e.g., *Onychonycteris*), archaeonycterids, some icaronycterids (e.g., *Icaronycteris menui*), and *Necromantis* (Gunnell et al., 2011; Hand et al., 2012; Smith et al., 2012). M2 in *Aegyptonycteris* is characterized by a broad, shallow U-shaped ectoflexus that is centered on the tooth directly adjacent to the centrocrista. This differs from the condition seen in most other Eocene bats, which have either a shallow ectoflexus with its deepest point centered more anteriorly between the parastyle and centrocrista (e.g., *Onychonycteris, Ageina, Icaronycteris, Hassianycteris, Palaeochiropteryx*), a much deeper ectoflexus (e.g., *Archaeonycteris, Necromantis*, philisids), two separate ectoflexi separated by the centrocrista (e.g., *Cecilionycteris*), or a notch between the parastyle and centrocrista (e.g., mixopterygids; Gunnell et al., 2011; Ravel et al., 2012; Hand et al., 2012; Smith et al., 2012). Some species of *Palaeophyllophora* (*P. nova, P. parva*) have a somewhat similar morphology on M2 but the U-shaped surface is shallower, resulting in a relatively straighter ectocingular border (Revilliod, 1917; Maitre, 2014).

Both molars in *Aegyptonycteris* preserve a strong, curved parastyle as occurs in most other Eocene bats (Gunnell et al., 2008, 2011; Smith et al., 2012). A curved metastyle is also present on M2 but is absent from M3, which also lacks a postmetacrista. Both molars in *Aegyptonycteris* have a complete centrocrista enclosing a narrow trigon (protofossa).

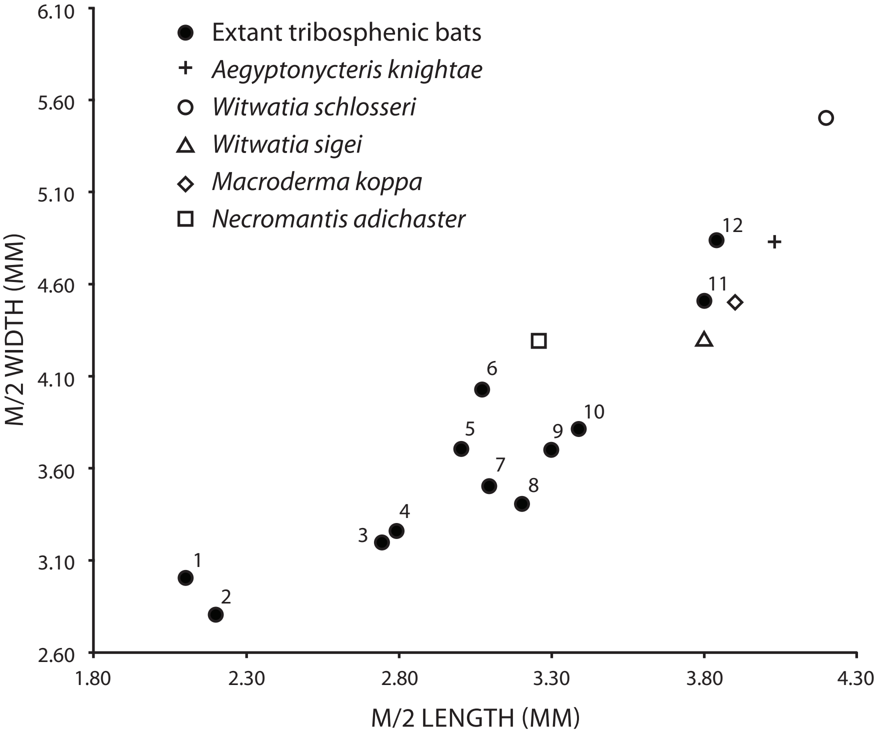

FIGURE 6. Bivariate plot of length vs. width of M2 in selected large extant and extinct bats with tribosphenic dentitions (see table 3 for body mass in living taxa). Extant bats include: **1**, *Saccolaimus peli* (Emballonuridae); **2,** *Taphozous nudiventris* (Emballonuridae); **3,** *Hipposideros commersoni* (Hipposideridae); **4,** *Eumops dabbenei* (Molossidae); **5,** *Hesperoptenus tickelli* (Vespertilionidae); **6,** *Artibeus fimbriatus* (Phyllostomidae); **7,** *Myotis* (Vespertilionidae); **8,** *Vampyrum spectrum* (Phyllostomidae); **9,** *Phyllostomus hastatus* (Phyllostomidae); **10,** *Megaderma lyra* (Megadermatidae); **11,** *Eumops perotis* (Molossidae); **12,** *Macroderma gigas* (Megadermatidae).

This is the same condition as seen in most early Paleogene bats (Gunnell et al., 2011; Smith et al., 2012) with the exception of philisids, which lack a contact between the postparacrista and premetacrista and thus have a trigon that is open on the labial side of the tooth (Gunnell et al., 2008). Both molars in *Aegyptonycteris* lack any trace of a mesostyle cusp at the juncture of the postparacrista and premetacrista. In this feature they resemble onychonycterids, icaronycterids, archaeonycterids, *Palaeophyllophora*, and *Necromantis* (Gunnell et al., 2012; Hand et al., 2012; Smith et al., 2012). A mesostyle is present in palaeochiropterygids, hassianycterids, and philisids, although it is often small (Gunnell et al., 2008; Ravel et al., 2012; Smith et al., 2012).

A unique feature of the molars of *Aegyptonycteris* is the presence of a neomorphic cusp located on the stylar shelf between the parastyle and centrocrista. This cusp is quite well developed on both M2 and M3. We here designate this cusp as an "ectostyle" to indicate our conclusion that it is not homologous with any cusp previously described for bats or other laurasiatherian mammals. The surface of the stylar shelf region is uneven along the edge of the crown on both molars, but the only well-defined structures in this area are the parastyle, ectostyle, and (on M2 only) the metastyle; no other cusps or cuspules are present.

A precingulum is present on both molars in *Aegyptonycteris*. This shelf, which extends from the preprotocrista (with which it is continuous) along the mesial base of the paracone to terminate labially at the parastyle, is wide on M2 and narrow on M3. The degree of development of the precingulae in *Aegyptonycteris* is unremarkable and similar to that seen in most Eocene bats (Gunnell et al., 2008, 2011; Hand et al., 2012; Smith et al., 2012; Maitre, 2014). A narrow postcingulum is present on M2 but not M3 in *Aegyptonycteris*. The M2 postcingulum is not continuous with any other crests or cusps, but instead forms an isolated, narrow shelf along the base of the metacone. This differs from the condition seen in icaronycterids, some archaeonycterids (e.g*., Archaeoncyteris brailloni*), and *Lapidochiropteryx*, in which the postcingulum is continuous with the postprotocrista (Russell et al., 1973; Smith et al., 2012). The isolated postcingulum on the M2 of *Aegyptonycteris* is most similar to that of *Archaeonycteris trigonodon*, in which the postprotocrista runs to the base of the metacone and thus is not continuous with the postcingulum (Gunnell et al., 2011).

The M2 in *Aegyptonycteris* lacks a lingual cingulum around the base of the protocone. Most Eocene bats have a complete or partial lingual cingulum, the posterior portion of which often forms a hypocone shelf or lobe (Gunnell et al., 2008; Ravel et al., 2011; Smith et al., 2012; Maitre, 2014). A lingual cingulum of some type (minimally forming a small hypocone shelf) is present in onychonycterids, icaronycterids, archaeonycterids, palaeochiropterygids, mixopterygids, philisids, and *Necromantis* (Gunnell et al., 2008; Hand et al., 2012; Smith et al., 2012). In contrast, some representatives of some modern families (e.g., *Vespertiliavus schlosseri*, an Eocene emballonurid) lack a lingual cingulum on M2 (Smith et al., 2012).

One of the most notable features of the M2 of *Aegyptonycteris* is the presence of a large, bulbous hypocone set low on the posterolabial corner of the tooth. This structure is unique among bats. Most Eocene bats have at least a trace of hypocone shelf or lobe on M2, and a few have a well-developed heel (e.g., mixopterygids, *Tachypteron, Necromantis, Palaeophyllophora nova*); however, a hypocone cusp is lacking in most of these taxa (Hand et al., 2012; Smith et al., 2012; Maitre, 2014). *Carcinipteryx*, a mixopterygid, has a small hypocone (Maitre et al., 2008; Smith et al., 2012). Extant bats (and fossil members of extant families) frequently have a well-developed hypocone shelf on M2, and some species have a well-developed cusp on the posterolingual edge of this shelf (e.g., *Pteronotus davyi*; Dávalos et al., 2014: P891). The hypocone in these taxa is typically formed from the expanded edge of the hypocone shelf, and the hypocone is connected to the protocone either by a single crest (postprotocrista) or two crests that intersect at an angle on the lingual edge of the tooth (postprotocrista and endoloph; Dávalos et al., 2014: P891). *Aegyptonycteris* is unique in having a large, bulbous hypocone that is set low on the flank of the protocone without being connected to it by crests.

As in most other Eocene bats, the M3 in *Aegyptonycteris* is a broad tooth with a well-developed protocone, paracone, parastyle, metacone, and protocone. In this it differs from *Necromantis*, *Mixopteryx*, and *Palaeophyllophora*, which lack a metacone (Maitre et al., 2008; Hand et al., 2012). M3 in *Aegyptonycteris* has a rounded hypocone shelf but no hypocone cusp. As noted above, it also has a prominent metaconule. The postparacrista is somewhat longer than the premetacrista, and the postmetacrista is entirely absent. In the latter respect *Aegyptonycteris* differs most other Eocene bats, which preserve at least a small portion of the postmetacrista (Smith et al., 2012). However, *Archaeonycteris trigonodon* and *Lapidochiropteryx* also lack a postmetacrista on M3 (Tong, 1997; Gunnell et al., 2011; Smith et al., 2012). *Necromantis, Mixopteryx*, and *Palaeophyllophora* lack both a postmetacrista and a premetacrista on M3 (Maitre et al., 2008; Hand et al., 2012). The centrocrista in *Aegyptonycteris* does not approach the labial margin of the tooth, a condition shared only with onychonycterids and *Palaeophyllophora* among Eocene bats (Maitre et al., 2008; Hand et al., 2012; Smith et al., 2012).

DISCUSSION

The suite of traits seen in *Aegyptonycteris knightae* is unique and justifies recognition of this taxon as a distinct chiropteran family, Aegyptonycteridae (type genus and species = *Aegyptonycteris knightae*).

Identification of Aegyptonycteris as a Bat: The only known specimen of *A. knightae* is the holotype, which consists of a portion of the maxilla including two molars and the anterior orbital floor and base of the zygomatic arch (figs. 3–5). Morphology of the maxilla is not particularly informative about phylogenetic affinities. A broad, flat anterior orbital floor and well-developed zygomatic arch is seen in many mammalian clades including bats, primates, tupaiids, dermopterans, erinaceid eulipotyphlans, and marsupials. In some members of these groups (e.g., many bats; omomyid primates; erinaceid eulipotyphlans), the roots of the molar teeth breach the dorsal surface of the orbital floor as they do in *Aegyptonycteris*. While morphology of the preserved parts of the maxilla is consistent with this taxon being a bat, it is not sufficient evidence to definitively place it in Chiroptera. As is typical in mammalian paleontology, it is dental morphology that is key.

The majority of Paleogene fossil bats are characterized by a relatively simple dilambdodont tribosphenic dentition (Russell et al., 1973; Van Valen, 1979; Hand et al., 1994; Simmons and Geisler, 1998; Gunnell and Simmons, 2005; Maitre et al., 2008; Gunnell et al., 2011; Ravel et al., 2011, 2015; Hand et al., 2012; Smith et al., 2012). Because such dentitions occur primitively in many mammalian lineages, it is sometimes difficult to determine whether a fragmentary fossil known primarily from teeth represents a bat or some other type of tribosphenic mammal (e.g., Sanchez-Villagra et al., 2007). Apparent mistakes have been made both ways: *Wyonycteris chalix* from the late Paleocene of North America was originally described as a bat (Gingerich, 1987) but is now thought to have affinities that lie outside Chiroptera, perhaps with adapisoriculids (Hand et al., 1994; Smith, 1995) or with nyctitheriids (Gingerich and Smith, 2006; Secord, 2008), whereas *Wallia scalopidens* was originally described as a proscalopid eulipotyphlan (Storer, 1984) but is now regarded as a probable bat (Legendre, 1985; Gunnell and Simmons, 2005). Probably because mammalian teeth arise via similar developmental pathways and have been subject to natural selection for function, it appears that morphological change in dental characters has effectively become saturated over time, leading to rampant homoplasy and functional convergence (Kangas et al., 2004; Dávalos et al., 2014). No dental synapomorphies serve to unambiguously identify chiropteran teeth and distinguish them easily from those of other mammals; rather, researchers must rely on evaluation of a suite of features when determining the identity (bat vs. non-bat) of incomplete fossils that are not associated with cranial or postcranial remains (Hand et al., 1994; Simmons, 1994; Gunnell and Simmons, 2005).

In the upper dentition, presence of a strongly W-shaped ectoloph is clearly plesiomorphic for Chiroptera, appearing in all Paleogene bats described to date in which the molar teeth are preserved (Russell et al., 1973; Hand et al., 1994; Simmons and Geisler, 1998; Gunnell and Simmons, 2005; Maitre et al., 2008; Gunnell et al., 2011; Ravel et al., 2011, 2015; Hand et al., 2012; Smith et al., 2012). Outside of bats, a W-shaped ectoloph also occurs in some marsupials, cynocephalid dermopterans, many nyctitheriids, tupaiids, plagiomenids, mixodectids, and eulipotyphlans including desmanids, talpids, and soricids (Hand et al., 1994; Ungar, 2010). The W-shaped ectoloph of *Aegyptonycteris* is clearly bat-like in its completeness and in the proportions of the four primary cristae (preparacrista, postparacrista, premetacrista, and postmetacrista). In general, bats have the paracone and metacone set relatively far lingually on the tooth crown, an arrangement that results in long primary cristae and a relatively buccolingually narrow trigon basin. This is the case in *Aegyptonycteris*. The labial slopes of the paracone and metacone in bats are often broad and long, forming wide parastylar and metastylar foveae, especially on M1–M2, and this is the condition seen in the M2 of *Aegyptonycteris*. However, because other mammals also exhibit many of these traits, detailed comparisons are warranted. Although the two teeth preserved in our specimen of *Aegyptoncyteris* apparently represent M2–M3, we include other loci in our comparisons below for the sake of completeness in cases where morphology of successive teeth varies.

Many nonbat mammals with dilambdodont molars have a mesostyle cusp at or near the junction of the postparacrista and premetacrista, but *Aegyptonycteris* and other relatively primitive Eocene bats (e.g., onychonycterids, icaronycterids, and archaeonycterids) lack evidence of a mesostyle. Instead, the premetacrista and postparacrista taper labially to join low on the crown with no cusp present. A number of families of derived crown-group bats (e.g., molossids, vespertilionids among others) often have a rounded labial projection that is formed at the confluence of the postpara- and premetacristae, but this projection is almost always developed as a smoothly rounded surface that does not form a distinct cusp and is not expanded mesiodistally. Other crown group bats lack any trace of a mesostyle entirely.

A few Cretaceous and Paleogene marsupials have weakly dilambdodont upper molars that show some development of a W-shaped ectoloph (Clemens, 1966; Cifelli, 1993; Godthelp et al., 1999; Rose, 2006). Among extant marsupial lineages, didelphids, dasyurids, and peramelemorphians are typically moderately to strongly dilambdodont (Archer, 1976; Travouillon et al., 2010, 2013, 2014). Marsupial dilambdodonty generally differs from that seen in bats in that the paracone and metacone are set very far lingually and the postparacrista and premetacrista are very short, producing a very broad stylar shelf and a buccolingually narrow protofossa that does not extend far onto the stylar shelf. Additionally, parastylar and metastylar foveae are not generally developed on marsupial molars, unlike the condition that is seen in virtually all dilambdodont bats. Bandicoots are an exception to this pattern; the postparacrista and premetacrista in these marsupials are very long, sometimes extending nearly to the labial margin of the tooth crown, and parastylar and metastylar foveae are well devoloped (Travouillon et al., 2010, 2013, 2014). However, bandicoots have a pair of large stylar cusps flanking the labial ends of the postparacrista and premetacrista, a condition that distinguishes them from bats, which generally lack these cusps (see below).

Cynocephalid dermopterans such as *Galeopterus variegatus* are somewhat similar to bats in having paracones and metacones that are lingually placed, but the bases of these cusps terminate in distinct paraconules and metaconules, which as noted earlier are rare in bats although a metaconule is present in *Aegyptonycteris*. The postparacrista and premetacrista of *Galeopterus* are relatively long and nearly parallel to each other, which in turn produces a protofossa that is relatively wide throughout. This condition is seen in bats only in Philisidae, and it does not occur in *Aegyptonycteris*, which has a narrow protofossa like the majority of bats. *Galeopterus* lacks any trace of a mesostyle, a condition similar to that seen in most bats.

Some nyctitheriids including *Wyonycteris* (see Smith, 1995; Gingerich and Smith, 2006) have molars with a weakly developed W-shaped ectoloph with a short postparacrista and premetacrista. In these forms the paracone and metacone are positioned relatively labially on the tooth crown, the preparacrista is very weakly formed, and the trigon basin is very wide buccolingually. This morphology is distinctly different from that seen in tribosphenic bats including *Aegyptonycteris*. Other nyctitheriids lack W-shaped ectolophs altogether (e.g., *Leptacodon*, see Secord, 2008), suggesting that any shared resemblances of upper dentitions between chiropterans and nyctitheriids are convergent in nature.

Scandentians such as *Tupaia* (e.g., *Tupaia glis*; *Tupaia dorsalis*) have upper molars characterized by a relatively mesiodistally elongate and buccolingually short W-shaped ectoloph in which the paracone and metacone are moderately lingually placed but are broadly separated to produce a very broad protofossa that is closed labially by an extensive rounded mesostyle. This differs significantly from the condition seen in most bats including *Aegyptonycteris*, which typically have a narrow, closed trigon and lack a mesostyle. The other scandentian family, Ptilocercidae lacks a W-shaped ectoloph entirely.

Mixodectids and plagiomenids (Szalay, 1969; Rose and Simons, 1977) have molars with a weakly formed W-shaped ectoloph in which the paracone and metacone are located near the labial margin of the tooth crown. These cusps are often basally inflated and the primary cristae are very short, quite unlike the condition seen in most bats including *Aegyptonycteris*. The mesostyle in mixodectids and plagiomenids, if present, is small and cuspate.

Desmans (e.g., *Galemys pyrenaicus*) have molars in which the paracone and metacone are located lingually as in bats, and have fairly well developed and broad parastylar and metastylar fovea as well. However, in desmans the postparacrista and premetacrista both terminate labially as distinct rounded cusps (paired mesostyles) that are separated from each other by a narrow extension of the protofossa. The protofossa in desmans extends to the labial border of the tooth, so the centrocrista is incomplete and the trigon is open labially. This condition differs significantly from the closed centrocrista seen in most bats including *Aegyptonycteris*. Philisids have a similar arrangement of cristae and an open centrocrista like those seen in desmans, but this condition is not seen in any other family of bats, living or extinct.

All talpids (e.g., *Euroscaptor micrura*, *Mogera wogura*, *Parascalops breweri*, *Scapanus latimanus*, *Talpa europaea*) have a W-shaped ectoloph, but members of this family exhibit variability in the form and arrangement of the primary cristae. In general, talpids differ from bats in that the cristae that form the "W" are very narrow, high, and sharply defined. The M1 almost always lacks a preparacrista in talpids, a condition different from that seen in bats, most of which have a well-developed preparacrista. In contrast to the M1, the M2 in talpids has a nearly symmetrical "W" that includes a high, rounded mesostyle at the junction of the centrocrista. The paracone and metacone are set in lingually on the crown but not as far as is typical of bats, leaving a relatively broader trigon basin and relatively shorter and more modest parastylar and metastylar fovea than are seen in bats, including *Aegyptonycteris*.

Like talpids, soricids (e.g., *Blarina brevicauda*, *Crocidura foetida*, *Crocidura negrina*, *Suncus murinus*) have a W-shaped ectoloph of variable design and expression. Typically the metacone is set farther lingually than the paracone on M1, and the metastylar fovea is more robust and larger than the parastylar fovea, producing an asymmetrical labial tooth crown quite different from that seen in most bats including *Aegyptonycteris*. The trigon is short and narrow, and the mesostyle tends to be robust and much more massive than is seen in any other bat.

Degree of development of the stylar shelf is another feature that can be compared across bats and other taxa with a W-shaped ectoloph. Dilambodont bats—including *Aegyptonycteris*—have upper molars characterized by a well-developed stylar shelf with a strong, curved or hooked parastyle, a strong metastyle, and a mesostyle that is either entirely absent or small. M1 and M2 are essentially homodont in most bats, without significant differences in terms of principal cusp development or placement on the labial tooth crown.

Other dilambdodont mammals differ from typical bats in the structures of their stylar shelves. Many extant didelphid marsupials (e.g., *Didelphis*, *Chironectes*, *Lutreolina*) as well as many Cretaceous and Paleogene fossil marsupials (Rose, 2006) develop extensive stylar shelves. In many cases (e.g., *Lutreolina*, *Chironectes*, herpetotheriid didelphimorphs) the stylar shelf may be as wide or wider than the lingual portion of the tooth, a condition never found in bats. Many marsupials also develop a number of accessory stylar cusps and cuspules (Simpson, 1929; Cifelli, 1993) that seldom occur in bats. Although *Aegyptonycteris* does have a single neomorphic "ectostyle" between the parastyle and centrocrista on the stylar shelf, we view this as not homologous with the "stylar cusp B" of marsupials, a structure that occurs in the same general position on some marsupial teeth (Bensley, 1906; Simpson, 1929; Clemens, 1966; Cifelli, 1993). The large stylar cusps (often labeled A through D) in marsupials are not regarded as homologous with any cusps on placental mammal teeth because they are absent in stem metatherians and eutherians (Clemens, 1966; Cifelli, 1993; Rose, 2006; Ungar, 2010). The isolated ectostyle set at the base of the parastylar fovea in *Aegyptonycteris* differs from stylar cusp B in most marsupials because it is not located on the labial margin the crown nor connected to the premetcrista, both of which are common morphologies in marsupials (Archer, 1976; Cifelli, 1993; Rose, 2006; Ungar, 2010; Travouillon et al., 2010, 2013, 2014).

Dermopterans (e.g., *Galeopterus*) essentially lack stylar shelves and have little or no stylar cusp development. Tupaiids have either a short, hooked parastyle (e.g., *Tupaia dorsalis*) or lack any inflection of the parastyle (e.g., *Tupaia glis*). They also have an elongate metastyle that is normally not hooked, and have a broadly rounded, mesiodistally extended, and weakly projecting mesostyle that closes the labial aspect of a relatively broad protofossa. The mesostyle may be smoothly rounded (*Tupaia dorsalis*) or may develop a small projection on the curved mesostylar surface (*Tupaia glis*).

Desmans (e.g., *Galemys*) have complex stylar shelves with a proliferation of cusps and ectoflexi. M1 differs markedly in structure compared to M2, especially in the mesiodistal length of the stylar foveae and in the positioning of the paracone (less lingual than the metacone on M1, equally lingually shifted on M2).

Talpids have a M1 with a much different form of stylar shelf than M2. The M1 essentially lacks a parastyle and preparacrista, while the metastylar area is expanded and the postmetacrista is often elongate and sharply crested to form a slicing blade (e.g., *Talpa, Euroscaptor, Mogera, Scapanus*). M2 generally has more equal-sized parastylar and metastylar fovea, and has either a short, curving parastyle and metastyle (e.g., *Scapanus, Parascalops*) or a short and straight parastyle and metastyle (*Talpa, Euroscaptor, Mogera*). The disposition of the mesostyle is similar in most moles with M1 having a more mesiodistally restricted and weakly projecting mesostyle while M2 has a more rounded and extended mesostyle that may be either weakly projecting (e.g., *Talpa*) or more strongly projecting (*Mogera, Scapanus*). The exceptions to this general pattern (e.g., *Euroscaptor, Parascalops*) have both M1 and M2 with broad and projecting mesostyles. Like bats, talpids do not have mesostyles that project beyond the labial extent of the parastyle or metastyle. In comparison to talpids, the M2 of *Aegyptonycteris* lacks any development of a mesostyle, has a more symmetrical stylar shelf, a much more buccolingually restricted protofossa, a more developed hooklike parastyle, and possesses both a hypocone and metaconule, in contrast to moles.

Soricids (e.g., *Blarina, Crocidura, Suncus*) similarly show a variety of stylar shelf morphologies. In contrast to talpids, however, M1 and M2 are much more similar to each other. The mesostyle in shrews tends to be more mesiodistally compressed compared to that of talpids, but in some cases (e.g., *Crocidura*) it may extend as far or farther labially than do the parastyle and metastyle. In general, stylar shelves and stylar fovea are more restricted buccolingually in shrews than in bats. The metacone and metastylar region are often larger relative to the paracone and parastylar area in shrews (*Blarina* and *Suncus* in particular). In virtually all archaic bats (including *Aegyptonycteris)* and in most extant dilambdodont bats the parastylar and metastylar regions of M1 and M2 are similar in size and proportions and show only a small amount of variation. Extant bats characterized by specialized dietary habits such as frugivory (e.g., stenodermantine phyllostomids) or nectarivory (e.g., glossophagine phyllostomids) often exhibit stylar shelf simplification and reduction (Freeman, 1995, 1998; Ungar, 2010).

Dilambdodont mixodectids and plagiomenids (Szalay, 1969; Rose and Simons, 1977) have buccolingually narrow stylar shelves with little or no parastylar or metastylar elongation. Mesostyles, if present are cuspate, not flattened projections. Some plagiomenids have a proliferation of stylar cusps (e.g., *Plagiomene, Worlandia*, see Rose, 2006) but determining whether any of them might be homologous to the ectostyle of *Aegyptonycteris* is not possible at this time. Mixodectids, on the other hand, tend to lack or have only very weakly developed parastylar and metastylar cusps. None of these taxa exhibit the well-developed parastyle and metastyle characteristic of bats including *Aegyptonycteris*.

Some nyctitheriids, such as *Wyonycteris* (Smith, 1995; Secord, 2008), have well-developed stylar shelves with buccolingually short stylar fovea. A narrow, cuspate mesostyle is present and it does not project beyond the labial border of the tooth. A short, hooked parastyle also is present and there is a modest development of a straight metastyle. Accessory cuspules may be developed along the labial border of the stylar shelf, and there is a modest, broad ectoflexus developed on M2 (Gingerich and Smith, 2006). Most of these features are decidedly unlike those of bats, although *Aegyptonycteris* does possess a single ectostyle. As noted above, another well-documented nyctithere, *Leptacodon* (Smith, 1996; Secord, 2008), has a narrow stylar shelf but lacks stylar foveae and a mesostyle, and does not have curving or extended stylar areas except for a modest elongation of the metastyle on M2.

Hand et al. (1994: 379) noted two "probable synapomorphies" of early bats: presence of a well-developed labial cingulid on the lower molars (unfortunately not preserved in our specimen of *Aegyptonycteris*) and marked reduction of the para- and metaconules on the upper molars. Most bats lack conules entirely (Russell et al., 1973; Gunnell et al., 2011; Hand et al., 2012; Smith et al., 2012; Ravel et al., 2012, 2015; Dávalos et al., 2014) although small metaconules are present in some onychonycterids, icaronycterids, and some palaeochiropterygids, and tiny paraconules are occasionally present in onychonycterids, icaronycterids, and archaeonycterids (Smith et al., 2012). In this context, the large metaconules seen in *Aegyptonycteris* are not a "batlike" trait. However, neither does the condition of the conules in *Aegyptonycteris* resemble that seen in other mammalian taxa that have a W-shaped ectoloph.

Paraconules and metaconules are common in the molar dention of many tribosphenic mammals (Ungar, 2010). Many marsupials have well-developed conules (Archer, 1976) that in some cases are quite large; many bandicoots, for example, are characterized by large metaconules that form a "metaconular hypocone" on the posterolingulal corner of the molar crowns (Travouillon et al., 2010, 2013, 2014). Presence of well-developed conules is believed to represent the plesiomorphic condition for marsupials (Archer, 1976). Cynocephalids, nyctitheriids, mixodectids, and desmans have paired conules that are well developed and subequal in size, and plagiomenids have paired, greatly inflated conules. Some other nonbat taxa with a W-shaped ectoloph lack or have only very small conules (some marsupials (e.g, extant didelphids), talpids, soricids, and tupaiids), so bats are not the only group to exhibit conule reduction. In this context, we interpret the condition in *Aegyptonycteris* as an incidence of mosaic evolution. The large metaconules in *Aegyptonycteris* may be either plesiomorphic—inherited from nonbat ancestors—or autapomorphic, possibly linked to the clearly derived enhancement of the distolingual corner of the tooth for crushing (as evidenced by the large, rounded hypocone on M2; see discussion below). The reduction of the paraconule is apparently a chiropteran feature that *Aegyptonycteris* shares with other bats, although it is a feature characteristic of some other groups as well.

The presence of a bulbous hypocone in *Aegyptonycteris* is an unusual trait, particularly since virtually all Eocene bats lack this cusp (Hand et al., 2012; Smith et al., 2012). Among extant bat lineages that have a hypocone, it is typically structurally different from that seen in *Aegyptonycteris*, formed from the raised edge of the hypocone shelf (e.g., many noctilionoids), from a crest that runs posterolincually down the flank of the crown from the postprotocrista, or as an isolated cusp that is separated from both the postprotocrista and the edge of the hypocone shelf (e.g., this variation is best observed in molossids; Legendre et al., 1988; Hand, 1990; Czaplewski et al., 2003; Dávalos et al., 2014: P891; personal obs., N.B.S., G.F.G.). However, in our opinion the bulbous hypocone in *Aegyptonycteris* is an autapomorphic trait and thus not informative about relationships. As noted by Hunter and Jernvall (1995), a hypocone—defined as a cusp on the distolingual corner of a tribosphenic tooth—has evolved over 20 times among mammals in the Cenozoic. Acquiring a hypocone is apparently both evolutionarily "easy" and adaptively significant since it increases occlusal area, in effect doubling the area devoted to crushing food (Hunter and Jernvall, 1995). As such, the hypocone has been described as a "key innovation in mammalian evolution" (Hunter and Jernvall, 1995: 10718). Given the vast array of dental morphologies known among bats (Freeman, 1984, 1988, 1998, 2000; Hand, 1990; Hand et al., 1994; Maitre et al., 2008; Gunnell et al., 2011; Ravel et al., 2011; Hand et al., 2012; Smith et al., 2012; Dávalos et al., 2014: P891), it is perhaps not surprising to find new features and combinations of traits in newly discovered ancient bat lineages.

Body Size: *Aegyptonycteris knightae* was clearly a large bat (fig. 6, table 3). In terms of M2 size, *A. knightae* is comparable to the extant phyllostomid *Vampyrum spectrum*, one of the largest-known echolocating bats with a body mass of approximately 170 grams. *Aegyptonycteris* has an M2 somewhat larger than *Macroderma gigas*, the Australian ghost bat, which has a body mass of about 125 grams. Among extinct bats, the M2 of *Aegyptonycteris* is equal in length to that of *Witwatia schlosseri,* but *W. schlosseri* is 0.7 mm wider (table 3, fig. 6). *W. schlosseri* is also found exclusively at Fayum locality BQ-2, interestingly indicating that this locality may have simultaneously supported at least two very large bats in the Late Eocene.

Body size plays a large role in most aspects of ecology and physiology of all mammals including bats (Richards, 1995; Speakman and Thomas, 2003; Swartz et al., 2003; Willig et al., 2003; McNab, 2007; Anderson et al., 2008). In bats, body size influences flight behavior, bite force, diet, foraging habits, roost selection, reproductive behavior, thermoregulation, migratory behavior, and many other aspects of biology (Swartz et al., 2003; Herrel et al., 2008; Giannini et al., 2012). Insectivorous bats that hunt by aerial hawking may be limited in body size due to constraints imposed by the physics of echolocation, flight performance, and limited abundance of large insect prey (Barclay and Brigham, 1991). Although this is a complicated relationship (Swartz et al., 2003) and some lineages have evolved species with larger body sizes, most chiropterans are relatively small (Giannini et al., 2012). The central tendency in size in extant bats, as estimated by the median value, is around 14 g (Giannini et al., 2012). However, size of bats as a group spans three orders of magnitude, ranging from 2–3 g in the smallest species to >1000 g in the largest taxa (Giannini et al., 2012).

Using data on midshaft diameters of long bones (e.g., humerus, radius, femur, and tibia), Giannini et al. (2012) estimated the body mass of several well-preserved Eocene fossil taxa and found that they ranged in size from relatively small (*Palaeochiropteryx tupaiodon*, 9–16 g) to relatively large (*Hassianycteris messelensis*, ~90 g). Some of the most primitive bats fall in between: *Onychonycteris finneyi* (39–41 g), *Icaronycteris index* (24–27 g), and *Archaeonycteris trigonodon* (29–31 g; Giannini et al., 2012). Optimizing body mass on the phylogenies of Simmons et al. (2008) and Hermsen and Hendrick (2008), both of which included fossils, they concluded that body size at the base of the bat tree was ~40 g, and that it decreased along the backbone of the tree to ~14 g by the base of the chiropteran crown clade or base of Microchiroptera, depending on the tree (Giannini et al., 2012). Optimization on the molecular trees of Teeling et al. (2005) and Eick et al. (2005) similarly indicated that the primitive body size for the chiropteran crown clade was 10–14 g (Giannini et al., 2012). Larger body sizes than the ancestral lineage were shown to have evolved at least 17 to 19 times in bats, while smaller body size evolved at least 11 to 17 times (Giannini et al., 2012). Among Eocene bats, larger body size has apparently evolved at least twice, once in *Hassianycteris* (Giannini et al., 2012) and again in the philisid *Witwatia* (Gunnell et al., 2008; Ravel et al., 2012, 2015). Assuming that *Aegyptonycteris* is not closely related to either *Hassianycteris* or *Witwatia*—which seems likely given their divergent dental morphologies—*Aegyptonycteris* appears to represent another case of gigantism (sensu Gould and MacFadden, 2004) in Eocene bats.

Dental Morphology and Diet: The structure of teeth in the mammalian dentition is highly correlated with diet (Freeman, 1984, 1988, 1998, 2000; Evans et al., 2007; Ungar, 2010; Santana et al., 2011a). For bats, researchers have long distinguished "animal-eating" or "animalivorous" taxa from those that feed partly or entirely on plant products (Freeman, 1984, 1998, 2000; Norberg and Fenton, 1988; Rex et al., 2010, Santana et al., 2011b). In this context, animalivory is an umbrella term that covers both insectivorous and carnivorous species, and those that fall somewhere in between (Freeman, 1984, 1998, 2000; Norberg and Fenton, 1988; Santana et al., 2011a, 2011b).

With respect to the molar dentition, dilambdodont cheek teeth that have high, pointed cusps and sharp cristae are generally indicative of an animalivorous diet (Freeman, 1988, 1998). In small animalivorous bats, the diet apparently usually consists mostly of insects and other arthropods (Norberg and Fenton, 1988; Kalka and Kalko, 2006, although also see Rex et al., 2010). As body size increases, some species with dilambdodont molar teeth often include small vertebrates in their diet. For example, large phyllostomines (e.g., *Vampyrum spectrum*, *Chrotopterus auritus*, *Trachops cirrhosus*), noctilionids (e.g., *Noctilio leporinus*), nycterids (e.g., *Nycteris grandis*), megadermatids (e.g., *Macroderma gigas*, *Megaderma lyra, Cardioderma cor*), and vespertilionids (e.g., *Antrozous palidus, Nyctalus lasiopterus*) variously consume small vertebrates including birds, lizards, frogs, fish, mice, and sometimes even other bats (Norberg and Fenton, 1988; Freeman, 1984, 1998; Dondini and Vergari, 2000; Santana et al., 2011a, 2011b). Body size alone does not predict carnivorous habits, however, since many midsized and some large animalivorous bats apparently do not feed on vertebrates but instead prey only on insects (e.g., *Saccolaimus peli, Hipposideros commersoni*, *Cheiromeles* spp.; Norberg and Fenton, 1988). Norberg and Fenton (1988) found that a combination of traits including use of low duty-cycle echolocation, medium or large body size (≥17 g), low aspect ratio wings (≤6.3), and low relative wing loading (<36) significantly distinguishes carnivorous species from those that consume only insect prey. However, the tiny "insectivorous" bat *Micronycteris microtis* (5–7 g) has recently been shown to occasionally capture and eat lizards (Santana et al., 2011b), indicating that even very small bats can take vertebrate prey. The ability to consume vertebrate prey apparently does not require large body size, although a predator must be large enough to overpower its prey and must have a sufficient gape and bite force to grasp, kill, and process it. Including vertebrates in the diet may actually have facilitated the evolution of larger body sizes in some lineages of animalivorous bats, rather than large body size being a requirement for carnivory (Hand, 1985; Freeman, 2000).

Carnivorous bats lack specialized carnassial teeth, but those that regularly eat vertebrate prey nonetheless show some dental modifications (Freeman, 1984, 1998). Evolution of carnivory in bats is typically associated with elongation of the metastylar shelf and relative elongation of the postmetacrista on M1 and M2 (Freeman, 1984, 1998; Hand, 1985). Large-bodied species that regularly include terrestrial vertebrate prey in the diet have proportionally longer crests (especially the postmetacrista) on the upper molars than their smaller insectivorous relatives (Freeman, 1984, 1998; Hand, 1985). For example, the postmetacrista on M1 and M2 is 1.5 to 2 times the length of the preprotocrista in the highly carnivorous *Vampyrum spectrum*, *Chrotopterus auritus*, *Megaderma spasma*, and *Macroderma gigas* (Freeman, 1988; Dávalos et al., 2014: P891). In concert with elongation of the postmetacrista, the paracone and metacone are often located closer together (Freeman, 1984, 1998), thus reducing the relative length of the postparacrista and premetacrista (Dávalos et al., 2014: P891). The W-shaped ectoloph in these species is highly asymmetrical on M1 and M2, which are usually the only teeth to preserve all four branches of the "W" (preparacrista, postparacrista, premetacrista, postmetacrista). In contrast, insectivorous bats (and those that are more omnivorous) typically have a more symmetrical W-shaped ectoloph in which the preparacrista and postmetacrista are subequal in length and the postparacrista and the premetacrista are subequal in length (Freeman, 1984, 1998). The "intraloph" (distance between the paracone and metacone on the same tooth) and "interloph" (distance between the metacone on one tooth and the paracone on the tooth behind it) are close to subequal in noncarnivorous bats, but the intraloph is much smaller than the interloph in carnivorous species (Freeman, 1984). These proportions vary by tooth locus, with M2–M3 typically showing the greatest difference between intraloph and interloph distances (Freeman, 1984). *Phyllostomus hastatus*, a large phyllostomid that eats small vertebrates occasionally but that is otherwise omnivorous (including insects, fruit, nectar, and pollen in its diet; Gardner, 1977; Vehrencamp et al., 1977) exhibits intraloph/interloph ratios more similar to insectivorous bats than does its more carnivorous relative *Vampyrum spectrum* (Freeman, 1984; Dávalos et al., 2014: P891).

Most bats have upper molars with a basal distolingual cingulum or shelf (sometimes called a hypocone basin or shelf even if no hypocone is present) and many have a hypocone (Slaughter, 1970; Freeman, 1998). The hypocone is typically formed from the crestlike edge of the distolingual cingulum and is typically small (Slaughter, 1970; Dávalos et al., 2014: P891). Slaughter (1970) proposed that the function of the molar cingulae is deflection of exoskeletal fragments (generated by chewing arthropod prey) from accidental insertion into the alveoli, thus protecting periodontal tissue. Carnivorous bats (e.g., *Macroderma, Vampyrum*) typically have a very large hypocone shelf or basin, but the hypocone itself is poorly developed or absent (Freeman, 1998; Dávalos et al., 2014: P891). This association is congruent with the observation of Hunter and Jernval (1995) that presence of a hypocone is incompatible with carnassiform upper molars since it disrupts occlusal contact between metacrista and paracristid, which are the primary shearing blades emphasized in carnivorous mammals. Possession of a well-developed hypocone is therefore generally thought to be associated with herbivory (including frugivory and other forms of plant eating) in mammals (Hunter and Jernval, 1995).

Plant-eating habits in bats mostly involve consumption of fruit or flower products although folivory and seed predation have also been documented in some species (Gardner, 1977; Kunz and Diaz, 1995; Nogueira and Perracchi, 2003). Specialized plant-eating bats occur in two extant chiropteran families: Pteropodidae and Phyllostomidae (Gardner, 1977; Freeman, 1988, 1995). The cheek teeth of pteropodids are too highly derived to be easily comparable with those of dilambdodont bats, and homologies of cusps on pteropodid molars are considered difficult or impossible to determine (Koopman and MacIntyre, 1980; Freeman, 2000). Phyllostomid nectarivores and frugivores, however, retain remnants of the dilambdodont pattern that generally allows assessment of cusp homologies although a few questions still remain (Freeman, 1988, 1995, 1998; Ungar, 2010; Dávalos et al., 2014: P891). The upper molars of nectarivorous phyllostomids are dilambdodont but characterized by a buccolingually narrow stylar shelf with the paracone and metacone located near the labial edge of the tooth to produce a flat, wide, W-shaped ectoloph (Freeman, 1995, 1998; Ungar, 2010; Dávalos et al., 2014: P891). No hypocone is present although there may be a hypocone shelf (Ungar, 2010; Dávalos et al., 2014: P891). The teeth of nectarivores generally appear buccolingually compressed such that each molar is considerably longer mesiodistally than it is wide (Freeman, 1998; Ungar, 2010; Dávalos et al., 2014: P891).

Frugivorous phyllostomids typically have upper molars with flat, bulbous crowns and lower, blunter cusps and crests than seen in animalivorous species (Ungar, 2010; Dávalos et al., 2014: P891). M1 and M2 are quadrate in occlusal outline, with greatly reduced stylar shelves and paracones and metacones that are located near the labial edge of the tooth (Freeman, 1988; Ungar, 2010; Dávalos et al., 2014: P891). Freeman (1998: 149) summarized the general proportions of nonpteropodid bat teeth as follows: "Generally, insectivores and carnivores have large teeth with large stylar shelves, frugivores have large teeth with the smaller stylar shelves, and nectarivores have small teeth with small to moderate stylar shelves." The shape of the ectoloph in frugivores ranges from a flat W-shape to a wavy crest that has been characterized as a "cookie cutter" due to its location on the labial edge of the tooth (Freeman, 1988, 1998; Ungar, 2010; Dávalos et al., 2014: P891). The protocone is well developed, and the central portion of the crown (talon + trigon) often forms a broad, shallow, longitudinal groove that extends the length of the crown in frugivorous phyllostomids (Ungar, 2010; Dávalos et al., 2014). A hypocone is variously developed in frugivorous species, ranging from well developed (e.g., *Dermanura gnomus, Sphaeronycteris toxophyllum*) to entirely absent (e.g., *Platyrrhinus* spp.; Dávalos et al., 2014: P891). Low, broad cusps—some that can be clearly homologized with those of dilambdodont tribosphenic molars and some that cannot—characterize the molar teeth of the most specialized frugivores, members of the Stenodermatinae (Freeman, 1988; Dávalos et al., 2014: P891)

The primitive dental formula for bats includes three upper molars (Slaughter, 1970; Koopman and MacIntyre, 1980) and all animalivorous bats retain all of these teeth (Freeman, 1988, 1995). Some bats, including some primitive Eocene taxa, have a W-shaped ectoloph on M3 (e.g., *Onychonycteris*; Gunnell et al., 2011), but the majority of bats lack a postmetacrista on M3. The ectoloph in these forms is either N-shaped (comprising a premetacrista, postparacrista, and preparacrista) or V-shaped (postparacrista and preparacrista only; Freeman, 1988, 1998; Dávalos et al., 2014: P891). The paracone is retained in all of these variants, but the metacone may be either present or absent depending on the degree of reduction of the tooth. Many animalivorous bats have an abbreviated M3 with a V-shaped ectoloph, but M3 is nonetheless a relatively large tooth whose buccolingual width approaches that of the premolars and anterior molar teeth (Freeman, 1988, 1995; Dávalos et al., 2014: P891). In contrast, frugivorous bats often have an M3 that is greatly reduced in size relatively to the other teeth (e.g., *Pygoderma*, *Sturnira*, some *Artibeus*) or is absent (e.g., all pteropodids, some *Artibeus*, *Ectophylla*, *Centurio*; Freeman, 1988; Giannini and Simmons, 2007; Dávalos et al., 2014: P891). When retained, the reduced M3 in specialized frugivores is often a nearly featureless peglike tooth (Dávalos et al., 2014: P891). Nectarivorous bats show a somewhat different pattern: while M3 is absent in some taxa (e.g., *Lichonycteris, Leptonycteris*), it retains an N-shaped ectoloph in most taxa (Freeman, 1995; Dávalos et al., 2014: P891). Like the other molar teeth in nectarivores, M3 is buccolingually compressed in occlusal outline (Freeman, 1995; Dávalos et al., 2014: P891).

The proverbial "elephant in the room" in discussions of bat dietary guilds is the fact that some bats utilize multiple food sources and may defy easy categorization into a single dietary guild (Gardner, 1977; Rex et al., 2010; Dumont et al., 2011). Carnivorous bats often eat insects; insectivorous bats may occasionally eat small vertebrates, fruit, or nectar; frugivorous bats may supplement their diets with insects; and nectarivorous bats may also eat insects and fruit (Howell, 1974; Gardner, 1977; Freeman, 2000; Mello et al., 2004; Frick et al., 2009; Rex et al., 2010; Dumont et al., 2011; Santana et al., 2011b; Clare et al., 2014; Novaes et al., 2015; Yohe et al., 2015). Diets of some (perhaps many) bat species may also shift dramatically with season (Howell, 1974; Sosa and Soriano, 1996; Mello et al., 2004; Richards et al., 2008; Rex et al., 2010; Clare et al., 2014). However, most bat species appear to have morphological specializations for fruit, nectar, or animal-based diets (Freeman, 1984, 2000; Dumont, 2003; Swartz et al., 2003, Winter and Von Helverson, 2003) and rely entirely or primarily on one type of food at least in some seasons of the year (Gardner, 1977; Freeman, 1984, 2000), thus allowing the categorizations described above. Clear exceptions exist, however—true omnivorous bats that routinely consume a variety of food types including both animal and plant products (Gardner, 1977; Arkins et al., 1999; Lloyd, 2001; Rex et al., 2010; Dumont et al., 2011; Clare et al., 2014; Yohe et al., 2015). These taxa all belong to the Neotropical family Phyllostomidae and the related New Zealand/Australian endemic family Mystacindae.

In analyses of the diets of over 50 phyllostomid species captured at field stations in Costa Rica and Ecuador, Rex et al. (2010) and Dumont et al. (2011) reported that a majority of species utilized foods from more than one trophic level (e.g., insects as well as fruit, or small vertebrates as well as insects). Over 30 species had diets that included both plant products and a significant percentage of insects in fecal samples analyzed (Rex et al., 2010; Dumont et al., 2011). Only a few stenodermatine taxa appeared to consume nothing but fruit (e.g., *Vampyressa bidens, Platyrrhinus infuscus, Enchisthenes hartii*), while only a few phyllostomines consumed nothing but insects during the periods sampled (e.g., *Tonatia saurophila, Micronycteris megalotis, Lophostoma carrikeri, Lampronycteris brachyotis*; Dumont et al., 2011). Comparisons of results of fecal analyses with nitrogen isotope levels from plants and bat tissues suggests that plant material is an important component of the diet in most putative animalivorous phyllostomids, and that insects are an important component of the diet in most putative frugivores and nectarivores (Rex et al., 2010). Dietary flexibility seems to be the rule, rather than the exception, among phyllostomids (Rex et al., 2010). This is also true of mystacinids (Arkins et al., 1999; Lloyd, 2001). Although various phyllostomid clades may have specialized successfully on distinct dietary types that are reflected in distinct suites of morphological and behavioral traits, they have not sacrificed their capacity to exploit a variety of food types (Rex et al., 2010; Dumont et al., 2011).

One particularly flexible species is *Glossophaga soricina* (7–12 g), a small phyllostomid that lives in habitats ranging from columnar cactus deserts to wet tropical rainforests, and which has been variously described as an obligate nectarivore (e.g., Heithaus et al., 1975), seasonal insectivore (e.g., Howell, 1974; Howell and Burch, 1974), mostly frugivorous (e.g., Willig, 1986), and as an omnivore (e.g., Henry and Stoner, 2011), depending on when and where the population was studied (Clare et al., 2014). Review of dietary studies and foraging behavior of *Glossophaga soricina* strongly suggests that it can flexibly switch between trophic niches (plant versus insect foods) and may do so regularly, hence it is best classified as a highly flexible omnivore (Clare et al., 2014). In terms of its dentition, *Glossophaga* is one of the less-derived "nectarivorous" bats studied by Freeman (1995)—it retains dilambdodont molars that are of moderate size, are only slightly buccolingually compressed, have a relatively large stylar shelf, and M3 is retained as a large tooth with a N-shaped ectoloph (Freeman, 1995; Dávalos et al., 2014: P891).

A large phyllostomid bat with perhaps an even larger array of items in its diet is *Phyllostomus hastatus* (78–110 g), long considered to be a classic omnivore (Gardner, 1977; Freeman, 1988; Santos et al., 2003; Santana et al., 2011a). *Phyllostomus hastatus* is known to include insects, fruit, pollen, nectar, flower parts, and small vertebrates in its diet (Ruschi, 1953; Howell and Burch, 1974; Gardner, 1977; Vehrencamp et al., 1977; Santos et al., 2003). In seasonally dry Cerrado habitats in Brazil, *P. hastatus* has been shown to have an eclectic diet including insects from at least eight orders and 28 families including beetles, ants, and roaches (Willig et al., 1993). Fruit of at least 20 genera of plants are consumed by this species (Ruschi, 1953). Howell and Burch (1974) found evidence in fecal pellets that these bats sometimes eat both fruit and insects in a single foraging bout, confirming observations based on stomach contents by Bates (1875) that Gardner (1977) attributed to *P. hastatu*s. Subsequently Starret and de la Torre (1964) reported finding fruit pulp, insect parts, and feathers mixed together in the stomach of a specimen taken in Costa Rica. *Phyllostomus hastatus* also feeds on flowers of *Parkia* and

Ceiba, which they apparently may consume whole (de Carvalho, 1960, 1961). It is not unusual to capture *P. hastatus* with their heads dusted with pollen (Tuttle, 1970; personal obs., N.B.S.).

The vertebrate prey of *P. hastatus* includes small birds and mammals including mice and other bats (Dunn, 1933; Ruschi, 1953; Goodwin, 1946). As noted earlier, although it is a large bat that eats small vertebrates, the molar teeth of *Phyllostomus hastatus* are more like those of insectivorous bats than those of specialized carnivorous bats (Freeman, 1984, 1988). Similarly, although *P. hastatus* eats fruit regularly, this species does not show any of the typical dental modifications associated with frugivory in bats (Freeman, 1988) other than having a well-developed, blunt hypocone. The upper M1 and M2 of *P. hastatus* are quadrate in form, have a strong W-shaped ectoloph that is symmetrical, the paracone and metacone are located near the middle of the tooth, the stylar shelf is broad, the protocone is well developed, and a moderate-sized hypocone shelf with well-developed, blunt hypocone is present (Dávalos et al., 2014: P891). M3 is present and has a V-shaped ectoloph; although this tooth is reduced in size mesiodistally, it retains a strong protocone and is subequal in buccolingual width to the anterior molar teeth (Dávalos et al., 2014: P891).

Given the context provided by the correlations between diet and molar morphology described above, what can we conclude about the diet of *Aegyptonycteris knightae*? First of all, *Aegyptonycteris* clearly does not exhibit any of the extremes of molar morphology associated with carnivory, frugivory, or nectarivory. The stylar shelf on M2 is wide and the ectoloph is strongly W-shaped, relatively symmetrical, and not flattened. *Aegyptonycteris* lacks: the asymmetry and elongated postmetacrista characteristic of carnivorous bats, the flattened W-shaped ectoloph and buccolingual compression of nectarivores, and the narrow stylar shelf, broad longitudinal basin, and "cookie cutter" ectoloph morphology common in frugivores. Indeed, the shape of the ectoloph and stylar shelf of *Aegyptonycteris* resembles that of many insectivorous and omnivorous bats. The paracone, metacone, and protocone in *Aegyptonycteris* are robust cusps but do not appear to have been particularly tall, nor do the cristae appear to have been unusually bladelike, again arguing against extreme specializations for carnivory despite its large size. The relatively bunodont nature of the molar crowns, extensive wear on the principal cusps (paracone, metacone, and protocone), quadrate tooth form, and presence of a large hypocone are unlike those of most strictly insectivorous bats and suggest that crushing functions were very important in the dentition of *Aegyptonycteris*. As noted by Hunter and Jernvall (1995), acquiring a hypocone increases occlusal area and effectively doubles the area devoted to crushing food. In a survey of nonvolant extant mammals with known diets, these authors found that presence of a hypocone is strongly correlated with having a plant-based diet or being a generalist (defined as including three or more food types in the diet; Hunter and Jernvall, 1995). Strictly animalivorous mammals very rarely have a hypocone (Hunter and Jernvall, 1995). In this context, we conclude that *Aegyptonycteris* was very likely an omnivore. Taking both its dental morphology and its relatively large body size into account, it seems likely that the diet of *Aegyptonycteris* might have included insects, small vertebrates, fruits, and flower products. In short, it may have been very much like *Phyllostomus hastatus* in its feeding ecology.

Aegyptonycteris apparently represents a new ecological niche among Eocene bats, which are otherwise thought to have been insectivorous and/or carnivorous based on their size, craniodental morphology, and the few cases in which stomach contents have been preserved (Simmons and Geisler, 1998; Simmons et al., 2008; Hand et al., 2012; Ravel et al., 2012). *Necromantis*, a large Eocene bat with a heavy dentition, was originally described as a carion eater (hence the name "death eater" coined by Weithofer, 1887), but no living bat is known to eat carion. More recent analyses including better-preserved specimens indicate that *Necromantis* was most likely an animalivous bat specialized for carnivory and bone crushing (Hand et al., 2012). Ravel et al. (2012) argued that *Witwatia*, an Eocene philisid known for its large size, robust jaw, large canines, and high, broad molar cusps, may have been well adapted for flesh eating and probably had an opportunistic diet including both insects and vertebrate prey. Following a functional analysis of philisid dental occlusion, Ravel et al. (2015) subsequently raised the possibility (based on body size and "complexity" of masticatory function) that *Witwatia* might have opportunistically taken fruit as well. While this cannot be ruled out, the absence of any trace of a hypocone in *Witwatia* suggests that it was not a dedicated omnivore. In our opinion, *Aegyptonycteris* represents the first truly omnivorous bat known from the Eocene—a "specialized generalist" that routinely included food from several trophic levels in its diet.

ON USE OF THE TERM "EOCHIROPTERA": Van Valen (1979: 109) named the Suborder Eochiroptera for basal bats including "Palaeochiropterygidae, Archaeoncyteridae, and probably Icaronycteridae and Archaeopteropodidae." He treated Eochiroptera as equal in rank to Megachiroptera and Mirochiroptera, and considered it to be ancestral to both of these groups. McKenna and Bell (1997) and Simmons and Geisler (1998) subsequently rejected use of Eochiroptera because it is paraphyletic, and instead retained only monophyletic higher taxa in classifying fossil bats. While noting that it is at best a paraphyletic assemblage, several recent authors have nonetheless continued to use the name Eochiroptera to collectively refer to the archaic bat families including Onychonycteridae, Icaronycteridae, Palaeochiropterygidae, Archaeonycteridae, Hassianycteridae, and Tanzanycteridae (e.g., Tabuce et al., 2005, 2009; Ravel et al., 2011, 2012, 2015; Smith and Smith, 2013; Yu et al., 2014). In this context Eochiroptera explicitly does not include Eocene taxa belonging to extant families (e.g., *Tachypteron*, thought to be an early member of Emballonuridae; Storch et al., 2002), nor does it include Philisidae, an Eocene/Oligocene family belonging to the extant superfamily Vespertilionoidea (Simmons and Geisler, 1998; Gunnell et al., 2008, 2012; Ravel et al., 2012, 2015).

Most paleontologists have long regarded most Eocene bats as archaic forms representing an early grade of chiropteran evolution, but opinions have differed concerning their relationships to each other and extant bat lineages (for a review, see Simmons and Geisler, 1998). O'Leary et al. (2013) recovered moderate support for a clade including *Icaronycteris* and *Onychonycteris*, but did not sample any other putative eochiropteran taxa. Taxonomically more comprehensive (in terms of extinct and extant bats sampled) analyses by Simmons and Geisler (1998), Gunnell and Simmons (2005), Simmons et al. (2008), and Hermsen and Hendrick (2008) convincingly demonstrated that Eochiroptera is either paraphyletic or polyphyletic, with various extinct Eocene bats being consecutive stem taxa to the crown chiropteran clade, relatives of various lineages within the extant crown clade, or some combination of the two.

In an apparent departure from the general consensus that this group is paraphyletic, Ravel et al. (2015: fig. 5) depicted "Eochiroptera" as a clade (comprising *Palaeochiropterteryx tupaiodon*, *Archaeonycteris brailloni*, and *Icaronycteris menui*) in a phylogenetic tree based on analysis of dental characters. The analysis was aimed at resolving relationships of Philisidae to other vespertilionoids, and the "eochiropterans" were designated as outgroups for the purposes of the study (Ravel et al., 2015). The grouping of these taxa together in a clade with a reported Bremer value of 1 in their final tree is unexplained; in the absence of other outgroups, this appears to be an artifact of how PAUP* draws trees when multiple outgroups are designated. The Ravel et al. (2015: fig. 5) tree is misleading because it implies monophyly of Eochiroptera, something that could not be tested given the data set employed (i.e., one with no nonbat outgroups). Perhaps to counteract this impression, Ravel et al. (2015) put the name in quotation marks ("Eochiroptera") throughout their text and figures. Nevertheless, casual readers of their tree will be left with the mistaken impression that "Eochiroptera" is monophyletic.

From the beginning, the name Eochiroptera has been used largely because these taxa are perceived to share a suite of primitive features that are different from those seen in more derived bats (Van Valen, 1979; Ravel et al., 2011). Ravel et al. (2011: 403) observed that:

> The "Eochiroptera" differs from modern bats in many primitive dental features. The upper molars are characterized by a subrectangular outline waisted mesiodistally, a strong and central protocone, a complete and isolated lingual cingulum, a distolingual lobe, and well-marked conules.

We would argue that these observations do not adequately reflect the mosaic nature of dental evolution among Eocene taxa (e.g., see dental descriptions above and Smith et al., 2012), nor does this summary take into account the extensive range of dental variation seen in extant clades such as Noctilionoidea (e.g., Dávalos et al., 2014: P891). No phylogenetic analysis to date has included detailed dental characters scored broadly across both extant lineages and most or all Eocene bat families, so we do not know the relationships of many Eocene taxa, nor what dental characters (if any) actually diagnose a more derived chiropteran crown clade or clades.

In terms of ecology, the long-held idea that all archaic bats were insectivorous (e.g., Hill and Smith, 1984; Simmons and Geisler, 1998) appears refuted by recent analyses of taxa such as *Necromantis*, *Witwatia*, and now *Aegyptonycteris*. It has been thought for some time that the sensory systems (and presumed foraging strategies) of various insectivorous Eocene taxa differed significantly, ranging from apparent nonecholocators (e.g., *Onychonycteris*; Simmons et al., 2008, 2010) through perch-hunting echolocators (e.g., *Icaronycteris Archaeonycteris*; Norberg, 1989; Simmons and Geisler, 1998), aerial insect hawkers (e.g., *Palaeochiropteryx*, *Hassianycteris*; Norberg, 1989; Habersetzer and Storch, 1989, 1992; Habersetzer et al., 1994; Simmons and Geisler, 1998), to taxa that apparently utilized highly derived high duty-cycle flutter-detecting systems (e.g., *Tanzanycteris*; Gunnell et al., 2003). While we have no idea what the echolocation capabilities of *Aegyptonycteris* might have been, this taxon clearly appears to have occupied a different ecological niche beyond those already known among members of other Eocene bat families. *Aegyptonycteris* probably used somewhat different foraging strategies and may have employed other sensory systems as well (such as olfaction and vision), as do extant bats that feed on plant products all or some of the time (Laska, 1990; Hessel and Schmidt, 1994; Theis et al., 1998; Luft et al., 2003; Korine and Kalko, 2005).

Given the known or hypothesized range of variation, it seems clear that putative "eochiropterans" cannot be conceived of as homogeneous in any sense of the word; indeed, they seem to share little in common with each other besides living in the early Paleogene and representing lineages that subsequently became extinct. Because extinct Eocene bat families exhibit considerable mosaic evolution in morphological traits, do not seem to have inhabited a uniform ecological niche, and do not form a monophyletic group, we argue against use of the name Eochiroptera to collectively refer to these taxa. Use of this term is misleading because it implies evolutionary relationships and/or uniformity that are not supported by what is now known about Eocene bats.

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APPENDIX 1

Extant Specimens Examined

MARSUPIALIA

Didelphidae

Caluromys derbianus (UMMZ 62702); *Chironectes minimus* (UMMZ 134025); *Didelphis albiventris* (UMMZ 125453); *Didelphis marsupialis* (UMMZ 63001); *Didelphis virginiana* (UMMZ 96858); *Lutreolina crassicaudata* (UMMZ 134019); *Philander andersoni* (UMMZ 80083); *Philander opossum* (UMMZ 115402).

DERMOPTERA

Galeopterus variegatus (UMMZ 117122).

SCANDENTIA

Ptilocercus lowii (YPM MAM 10179); *Tupaia dorsalis* (UMMZ 174651); *Tupaia glis* (YPM MAM 10262).

EULIPOTYPHLA

Talpidae

Euroscaptor micrura (UMMZ 112537); *Galemys pyrenaicus* (UMMZ 97323); *Mogera wogura* (UMMZ 45841); *Parascalops breweri* (UMMZ 106264); *Scapanus latimanus* (UMMZ 99292); *Talpa europaea* (UMMZ 77608).

Soricidae

Blarina brevicauda (UMMZ 146901); *Crocidura foetida* (UMMZ 175105); *Crocidura negrina* (UMMZ 158881); *Suncus murinus* (UMMZ 118393).

CHIROPTERA*

Rhinolophidae

Rhinolophus acuminatus (SMF 33.817); *Rhinolophus alcyone* (FMNH 165148; ROM 46799); *Rhinolophus andersoni* (SMF 28.883); *Rhinolophus blasii* (FMNH 102369; ROM 64983); *Rhinolophus bocharicus* (SMF 27.052); *Rhinolophus capensis* (SMF 21.316); *Rhinolophus clivosus*

(AMNH 16157; ROM 38283; SMF 19.557); *Rhinolophus darlingi* (AMNH 257158; ROM 38346; SMF 79.623, 79.642); *Rhinolophus deckenii* (ROM 35302); *Rhinolophus denti* (ROM 77846); *Rhinolophus eloquens* (FMNH, 2650; ROM 77857); *Rhinolophus euryale* (ROM 77835); *Rhinolophus ferrumequinum ferrumequinum* (SMF 45.874, 45.876; ROM 77742); *Rhinolophus fumigatus* (ROM 65916); *Rhinolophus hildebrandtii* (AMNH 83922, 216210; ROM 68504); *Rhinolophus hillorum* (ROM 86948); *Rhinolophus hipposideros* (ROM 35322); *Rhinolophus landeri* (ROM 36308); *Rhinolophus maendelo* (SMF 79.643); *Rhinolophus mehelyi* (ROM 77837); *Rhinolophus simulator* (AMNH 257169); *Rhinolophus swinnyi* (SMF 82.202).

Hipposideridae

Asellia tridens (FMNH 152610; ROM 54785); *Cleotis percivali* (ROM 41778); *Hipposideros abae* (AMNH 49114, 49146); *Hipposideros ater* (ROM 40734); *Hipposideros bicolor* (ROM 77921); *Hipposideros caffer* (AMNH 55572, 114475; ROM 54773); *Hipposideros camarunensis* (AMNH 236304); *Hipposideros commersoni* (RBINS 7062; FMNH 152632; ROM 79665); *Hipposideros curtus* (ROM 54921); *Hipposideros cyclops* (AMNH 49093; ROM 75626); *Hipposideros fulginosus* (AMNH 257050); *Hipposideros gigas* (AMNH 241045); *Hipposideros marungensis* (AMNH 218967); *Hipposideros megalotis* (AMNH 219738; ROM 65818); *Hipposieros ruber* (AMNH 49110, 49182; ROM 86924); *Hipposideros speoris* (AMNH 208141); *Triaenops afer* (AMNH 207083, 237340); *Triaenops funculus* (ROM 42712); *Triaenops persicus* (ROM 71906).

Megadermatidae

Cardioderma cor (AMNH 184339; SMF 79.531, 74.245); *Lavia frons* (AMNH 54410; SMF 26.873); *Macroderma gigas* (AMNH 162669); *Megaderma lyra* (AMNH 208823; RBINS 201B); *Megaderma spasma* (AMNH 109285).

Rhinopomatidae

Rhinopoma hardwickii (AMNH 54405, 219721); *Rhinopoma macinnesi* (AMNH 219722).

Emballonuridae

Coleura afra (AMNH 82237; ROM 64112); *Emballonura alecto* (FMNH 47032; ROM 43674); *Emballonura atrata* (ROM 42056); *Emballonura monticola* (FMNH7 7010; ROM 38772); *Saccolaimus peli* (AMNH 86768; RBINS 24617); *Taphozous hildegardeae* (AMNH 219130; ROM 78060); *Taphozous longimus* (ROM 37968); *Taphozous nudiventris* (AMNH 27391; RBINS IG 1814).

Myzopodidae

Myzopoda schliemanni (FMNH 187665).

Phyllostomidae

Artibeus fimbriatus (UMMZ 146452); *Phyllostomus hastatus* (UMMZ 160617); *Vampyressa pusilla* (UMMZ 133730, 133731); *Vampyrum spectrum* (AMNH 18707).

Molossidae

Chaerophon bivittattus (AMNH 184418, 184419); *Chaerophon plicatus* (AMNH 27372); *Tadarida aegyptiaca* (AMNH 217023, 245636); *Eumops dabbenei* (UMMZ 126476); *Eumops glaucinus* (AMNH 179948); *Eumops perotis* (UMMZ 125381); *Mops leucostigma* (AMNH 170640); *Mops midas* (AMNH 184388); *Mops orientis* (AMNH 184410); *Myopterus daubentonii* (AMNH 48854); *Otomops martiensseni* (AMNH 88115, 172858); *Platymops setiger* (AMNH 217024); *Promops centralis* (AMNH 269114); *Sauromys petrophilus* (AMNH 165942); *Scotorepens sanborni* (AMNH 104835).

Vespertilionidae

Antrozous pallidus (AMNH 31173); *Chalinolobus gouldii* (AMNH 197234); *Corynorhinus rafinesquii* (AMNH 74902); *Eptesicus furinalis* (AMNH 235371); *Falsistrellus mackenziei* (AMNH 197222); *Hesperoptenus tickelli* (UMMZ 172254); *Lasionycteris noctivagans* (AMNH 130229, 140425); *Lasiurus borealis* (AMNH 134921, 144815); *Lasiurus cinereus* (AMNH 214126); *Lasiurus intermedius* (AMNH 253712); *Lasiurus seminolus* (AMNH 139871); *Myotis ater* (SMF 88.662); *Myotis bechsteini* (SMF 82.968); *Myotis blythii* (SMF 34.235, 47.776,43.391, 90.872, 49.233, 38.912; ROM 78744); *Myotis bocagei* (ROM 83948); *Myotis capaccini* (SMF 36.960); *Myotis daubentonii* (ROM 35679); *Myotis emarginatus* (SMF 38.916, 50.429, 59.656); *Myotis formosus* (SMF 58.751); *Myotis myotis* (SMF 78.311; ROM 35345; UMMZ 123523); *Myotis nattereri* (ROM 102812); *Myotis scotti* (SMF 49.594); *Myotis tricolor* (ROM 78625); *Myotis weltwitschii* (ROM 91210); *Murina suilla* (AMNH 234207); *Neoromicia rendalli* (AMNH 184356); *Otonycteris hemprichi* (AMNH 212071); *Rhogeessa tumida* (AMNH 182924); *Scotoecus albofuscus* (AMNH 237386); *Scotoecus hirundo* (AMNH 184460); *Scotomanes ornatus* (AMNH 56889); *Scotophilus dinganii* (AMNH 257434); *Vespadelus caurinus* (AMNH 162705).

Miniopteridae

Miniopterus australis (SMF 30.178); *Miniopterus gleni* (SMF 83.522); *Miniopterus majori* (SMF 89.116); *Miniopterus medius* (SMF 44.665); *Miniopterus pusillus* (SMF 65.199); *Miniopterus schreibersi* (AMNH 218977).

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* In addition to the specimens listed here, we also made comparisons with many species of noctilionoid bats documented in the illustrated data matrix of dental characters published by Dávalos et al. (2014) and made available online in MorphoBank (www.morphobank.org) as project P891.

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