

An evening bat (Chiroptera: Vespertilionidae) from the late Early Eocene of France, with comments on the antiquity of modern bats

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Abstract: Bats are among the most numerous and widespread mammals today, but their fossil record is comparatively meagre and their early evolution poorly understood. Here we describe a new fossil bat from dental remains recovered from late Early Eocene sediments at Prémontré, northern France. This 50 million-year-old bat exhibits a mosaic of plesiomorphic and apomorphic dental features, including the presence of three lower premolars, a single-rooted p3, short p4 with metaconid, myotodont lower molars and a tall coronoid process of the dentary. This combination of features suggests it is an early member of Vespertilionidae, today's most speciose and geographically widespread bat family. The Prémontré bat has bearing on hypotheses about the origins of vesper or evening bats (Family Vespertilionidae), as well as crown-group chiropterans.

Keywords: Western Europe, Ypresian, dental morphology, evolution, palaeobiogeography

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INTRODUCTION

One fifth of all extant mammal species are bats (Simmons, 2005a) but their fossil record is poor, with an estimated 66–81% of their fossil history missing (based on ghost lineage analysis and molecular divergence dates as well as phylogeny-independent statistical methods; Teeling *et al.*, 2005; Eiting & Gunnell, 2009). Identifiable bats first appear in the fossil record in the earliest Eocene ~55 Ma in Europe (Tabuce *et al.*, 2009); older chiropterans have been predicted by molecular data and combined data analyses (e.g., Bininda-Emonds *et al.*, 2007; Meredith *et al.*, 2011; O'Leary *et al.*, 2013) but these remain unrecognized. The oldest fossil bats have unspecialised dentitions, similar to those of many other Paleocene-Eocene mammals (e.g., nyctitheriids, lipotyphlans, adapisoriculids), but skeletal adaptations indicate they could fly and most could echolocate (Habersetzer & Storch, 1987; Haberstezer *et al.*, 1994; Simmons *et al.*, 2008). These early bats are referred to several extinct families whose relationships to each other and modern lineages are unclear (Simmons & Geisler, 1998; Simmons *et al.*, 2008; O'Leary *et al.*, 2013). A probable Laurasian origin for Order Chiroptera is generally accepted (e.g., Gunnell & Simmons, 2005), but there remains debate about when, where, and how modern bat families originated (Eick *et al.*, 2005; Teeling *et al.*, 2005; Ravel *et al.*, 2011, 2014, 2015; Smith *et al.*, 2012; Yu *et al.*, 2014). Molecular data suggest that most of the 20 modern bat families had evolved by the end of the Eocene (Teeling *et al.*, 2005; Simmons, 2005b; Miller-Butterworth *et al.*, 2007) but empirical/fossil data are scarce.

The fossil locality of Prémontré in the department of Aisne, northern France (Fig. 1), is known for its rich assemblage of terrestrial and marine vertebrates of late Early Eocene age (late Ypresian, 50 Ma; Dégrémont *et al.*, 1985; Escarguel, 1999; Adnet & Cappetta, 2008). It has produced one of the

most diverse Eocene faunas in the Paris Basin (Dégrémont *et al.*, 1985; Louis, 1996) and is especially rich in small mammals, which are represented by numerous isolated teeth and dentary fragments. The most abundant mammals in the Prémontré deposit are primates (Godinot *et al.*, 1992), rodents (Escarguel, 1999), pantolestids (Smith, 2001) and bats, but rarer multituberculate, marsupial, nyctitheriid, adapisoricid, apatemyid, hyaenodontan, miacid, condylarth, perissodactyl and artiodactyl teeth also occur (Dégrémont *et al.*, 1985; Sudre & Erfurt, 1996).

The Prémontré vertebrate fossils were recovered by members of the Société Laonnaise de Paléontologie in 1980–90 from a deposit located within the grounds of the 18th Century Prémontré Abbey (now a hospital), in sediments regarded to be a lateral equivalent of the Argile de Laon and of latest Ypresian age (biozone NP12) (Dégrémont *et al.*, 1985; Lecomte, 1994; Steurbaut, 1998; Adnet & Cappetta, 2008). They occur in sandy estuarine sediments (Sables de Glennes) associated with numerous selachian teeth (Cappetta, 1992; Adnet & Cappetta, 2008) as well as bony fish, plants and invertebrates (Dégrémont *et al.*, 1985, fig. 1). The Prémontré mammal taxa are correlated with reference-level MP10 of the mammalian biochronological scale for the European Paleogene (~50 Ma; Godinot *et al.*, 1992; Lecomte, 1994; Sudre & Erfurt, 1996; Escarguel, 1999).

Dégrémont *et al.* (1985: p.16) noted that several bat taxa are represented in the Prémontré deposit as follows: *Icaronycteris* sp. indet. (common), cf. *Archaeonycteris* (rare), and a small bat whose lower molars possess a distinctive myotodont structure (rare). Here we describe the small Prémontré bat with myotodont molars as an early member of the family Vespertilionidae. Collectively known as vesper or evening bats, vespertilionids today have a global distribution (except polar regions) and number ~400 species or nearly a third of all living bats (Simmons, 2005a). The new fossil chiropteran extends the origin of this enormous radiation back to 50

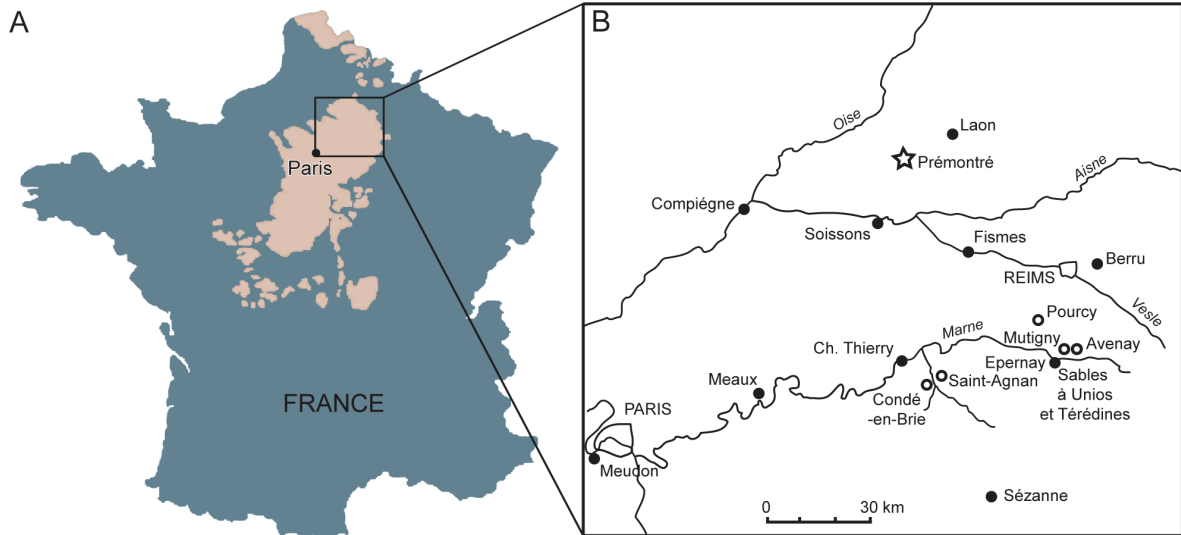


Figure 1. Map showing (A) Paleogene and Neogene sediments in the Paris Basin, and (B) location of Prémontré and other Ypresian mammal-bearing localities (open circles) noted in text (after Aubry *et al.*, 2005 and Louis, 1996).

Ma from 34 Ma (Gunnell *et al.*, 2008), with biogeographic inferences for modern bat origins, and provides an independent test of molecular clock divergence times for vespertilionids.

Institutional abbreviation. PL PRE, Pierre Louis Prémontré collections, Muséum National d’Histoire Naturelle, Paris, France; SLP, Société Laonnaise de Paléontologie collections, Muséum National d’Histoire Naturelle, Paris, France. A list of comparative materials and other institutional abbreviations is given in Appendix 1.

Dental terminology follows Hand *et al.* (2015), in which the three lower premolars are numbered p2, p3 and p4, and see Fig. 2.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Order CHIROPTERA Blumenbach, 1779
 Superfamily VESPERTILIONOIDEA Gray, 1821
 Family VESPERTILIONIDAE Gray, 1821
Premonycteris gen. nov.

Type species. *Premonycteris vesper* sp. nov.

Generic diagnosis. As for the type species until others are recognized.

Generic etymology. After the fossil locality Prémontré and *nycteris*, bat, alluding to an early signal or premonition about modern bats

Premonycteris vesper sp. nov.

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(Figs 3-4)

Holotype. SLP 29 BS 193; partial left dentary with p3, p4 and m1, alveoli for p2, m2-3, partial alveolus for c1, and most of ascending ramus (Fig. 3).

Referred specimens. SLP 29 PE 875, right dentary fragment with m2 and ascending ramus nearly complete (Fig. 4A-A’, C, D); SLP 29 PE 110, right dentary fragment with m1; SLP 29 PE 614, right dentary fragment with m2 (Fig. 4B); SLP 27 PR 8, right m2 (Fig. 4E, F-F’, G, H); PL PRE 273, right m1; PRE 347, right ?m1; PL PRE 611, left m2 (Fig. 4I, J-J’, K, L); PL PRE 1136, left ?m2; PL PRE 764, right m1; SLP 43 PR 17, right m2; PL PRE 1076, left m1; SLP 29 PE 369, left m3 (Fig. 4M, N-N’, O, P); SLP 29 PE 290, left m3.

Type locality and age. Prémontré, Aisne, north-eastern Paris Basin, France; Sables de Glennès; late Ypresian, Early Eocene (MP10 of the mammalian biochronological scale for the European Paleogene).

Etymology. *vesper*, from the common name for members of the family Vespertilionidae; Latin for evening.

Differential diagnosis. Differs from onychonycterids, icaronycterids, archaeonycterids, palaeochiropterygids, hassianycterids and mixopterygids (see included taxa and diagnoses in Smith *et al.*, 2012) and *Australonycteris clarkae*

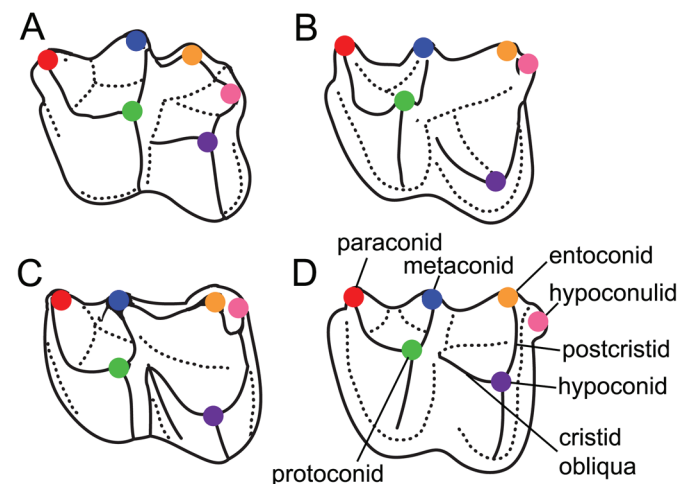


Figure 2. Lower molar structure: A, necromantodonty, B, nyctalodonty, C, submytodonty, and D, mytodonty (after Maitre, 2014).

in its single-rooted p3, short p4 and myotodont lower molars (Hand *et al.*, 1994). Differs from *Stehlinia* spp. (regarded to be palaeochiropterygids but see Smith *et al.*, 2012 and below) in its single-rooted p3 and myotodont molars. Differs from *Necromantis* spp. (Hand *et al.*, 2012; Maitre, 2014) in its large (rather than tiny) p3, short p4 with metaconid and myotodont molars. Differs from *Tachypteron franzeni* Storch *et al.*, 2002 in its single-rooted p3 and myotodont molars. Differs in its myotodont lower molars from other early Eocene bat taxa known from m1 or m2: *?Archaeonycteris praecursor* Tabuce *et al.*, 2009, Silveirinha, Portugal; *?Archaeonycteris* sp., Meudon, Paris Basin (Russell *et al.*, 1988); Eochiroptera indet. 2 (Marandat, 1991: pl. 5), Fournes, southern France; chiropteran indet. from Laguna Fria, Argentina (Tejedor *et al.*, 2005); eochiropteran from El Kohol, Algeria (Ravel *et al.*, 2011: fig. 4).

Differs from emballonuroids (emballonurids, nycterids), rhinopomatids and most rhinolophoids (hipposiderids, megadermatids, craseonycterids) in having three lower premolars, short p4 with metaconid and myotodont lower molars. Differs from rhinolophids in its large p3, short p4 with metaconid and myotodont molars.

Among noctilionoids, differs from noctilionids and mystacinids in having three lower premolars. Differs from mormoopids in its large but single-rooted p3 and p4 with metaconid. Differs from phyllostomids in its p4 with tall metaconid and from most species additionally in its myotodont molars. Differs from myzopodids in its large p3 and p4 with metaconid. Differs from thyropterids in its single-rooted p3, and from furipterids in its myotodont lower molars. Differs from both in its condyloid process of dentary being lower than coronoid process. Differs from extinct speonycterids in its large p3 with one root and myotodont lower molars.

Among vespertilionoids, differs from miniopterids in its myotodont molars, $p4=p3>p2$ and tall coronoid process. Differs from natalids in its myotodont molars, single-rooted p3, $p4=p3>p2$, and condyloid process lower than coronoid process. Differs from molossids and extinct philisids in presence of p3.

Differs from other vespertilionids by the following combination of characters: three lower premolars; $p4=p3>p2$; p2 and p3 with one root each; p4 two roots; p4 molariform with paraconid and metaconid and short heel; p4 conspicuously shorter than m1; lower molars myotodont (where the postcrisid directly joins the hypoconid to the entoconid isolating the hypoconulid; Fig. 2D); entoconid tall; postcrisid relatively low; hypoconulid small, lingual and low; cristid obliqua meets trigonid at centre of crown; trigonid and talonid widths similar; m3 talonid only moderately reduced in width; m3 hypoconulid present; dentary with tall ascending ramus and coronoid process higher than condyloid process; well-developed, laterally inflected angular process.

Description

The horizontal (mandibular) ramus (SLP 29 BS 193, SLP 29 PE 875; Figs 3-4) is shallow, with a straight ventral margin, mental foramen beneath p2, a narrow symphysis extending posteriorly to p2, and has a maximum depth of 1.5 mm (approximately equivalent to m1 height). The dentary has a tall ascending ramus, with the condyloid process occurring at the level of the tooth row and conspicuously lower than the tall coronoid process. The anterior edge of the coronoid rises nearly vertically, then curves posterodorsally near its (missing) tip. The well-defined angular process is slightly laterally

inflected and occurs just dorsal to the ventral margin of the dentary. An elongate mandibular foramen opens at the level of the tooth row.

The dental formula is $i?, c1, p2, p3, p4, m1-3$, where p2 and p3 are single rooted and p4 has two roots, all aligned in the tooth row (SLP 29 BS 193, SLP 29 PE 110, SLP 29 PE 875, SLP 29 PE 614). The p4 is conspicuously shorter than m1 (55% of m1 length; Table 1) and of similar length to p3 but wider. The minimum length of p2 is 0.5 mm based on alveolus length. The p3 is single rooted (confirmed by microCT; Fig. 3C) but with a clear longitudinal groove in the lingual face of the root. The p3 protoconid is worn but similar in height to p4, and is surrounded by a more or less continuous cingulid interrupted by a small anterolingual cusp; p3 lacks a metaconid. The p4 has a metaconid and paraconid (both much lower than the protoconid), a short heel and continuous anterior, buccal and posterior cingulids.

The m1 (SLP 29 BS 193, SLP 29 PE 110, PL PRE 273, PL PRE 764, ?PRE 347; Fig. 3) is longer than wide, with the trigonid and talonid of similar widths. In the trigonid, the protoconid is the tallest cusp, and the paraconid well developed but not as tall as the metaconid. The talonid exhibits the myotodont condition (where the postcrisid directly joins the hypoconid to the entoconid thereby isolating the hypoconulid); the hypoconulid is small and low. The postcrisid is low and the cristid obliqua is inflected anteriorly before meeting the trigonid in the centre of the tooth. The anterior, buccal and posterior cingulids are narrow but continuous, and there is no lingual cingulid. The posterior root is thicker than the anterior root. The m2 (SLP 29 PE 875, SLP 29 PE 614, SLP 27 PR 8, PL PRE 611, PL PRE 1136, SLP 43 PR 17; Fig. 4) is very similar to m1, but differs in its better developed paraconid and more anteroposteriorly compressed trigonid. With respect to m1 and m2, m3 (SLP 29 PE 290, SLP 29 PE 369; Fig. 4) is similar in trigonid length and width, and only moderately reduced in talonid width. The entoconid is relatively lower, the entocristid at a slight angle to the long axis of the tooth and the postcrisid at right angles to the entocristid.

Measurements of *Premonycteris vesper* are given in Table 1.

Gunnell *et al.* (2009) developed a set of algorithms to estimate body mass in extinct bats, based on dental, skeletal and weight measurements in 1,160 extant bats representing eight families (including Vespertilionidae). Using the proxy of lower first molar (m1) area and data in Gunnell *et al.* (2009: table 1), we estimated the weight of *Premonycteris vesper* to be 9.5 g, suggesting a relatively small bat, compared with the median value of 13.8 g for 905 extant bat species, and 3 to 50 g for living vespers (Smith *et al.*, 2004; Gunnell *et al.*, 2009).

DISCUSSION

A combination of dental features appears to exclude *Premonycteris vesper* from the extinct Eocene bat families Onychonycteridae, Icaronycteridae, Archaeonycteridae, Palaeochiropterygidae, Hassianycteridae, Mixopterygidae and Philisidae. This combination includes the presence of three lower premolars where $p4=p3>p2$, a large single-rooted p3, short p4 with metaconid, and myotodont lower molars (see Differential diagnosis above; and Table 2). A maximum of three upper and three lower premolars occurs in bats, but many lineages have subsequently lost one or two additional premolars (Table 2). In *Premonycteris vesper*, the retention of three lower premolars

is shared (probably plesiomorphically) with onychonycterids, icaronycterids, archaeonycterids, hassianycterids and palaeochiropterygids, as is presence of a metaconid on p4 shared with at least onychonycterids, icaronycterids, archaeonycterids and hassianycterids. The relative sizes of the premolars in *Premonycteris vesper* are more similar to those of icaronycterids, archaeonycterids, hassianycterids and palaeochiropterygids than to onychonycterids in which p3 is generally smaller than p4 and p2 (Smith *et al.*, 2012; Hand *et al.*, 2015; Table 2).

The higher level taxonomy of a number of Eocene bat taxa

remains in flux. *Stehlinia* species from the Middle Eocene to Late Oligocene of Europe were originally referred to the modern family Vespertilionidae (e.g., Revilliod, 1920) but subsequently transferred to the extinct Palaeochiropterygidae (e.g., Maitre, 2014). Palaeochiropterygidae has been included in Vespertilionoidea (e.g., Russell & Sigé, 1970; Sigé, 1997; Maitre, 2014), but was found to be the immediate sister group of the modern crown-group Chiroptera in phylogenetic analyses (e.g., Gunnell & Simmons, 2005; Simmons *et al.*, 2008). *Lapichiropteryx xiei* from Middle Eocene of China is referred to Palaeochiropterygidae (Tong, 1997). However, the

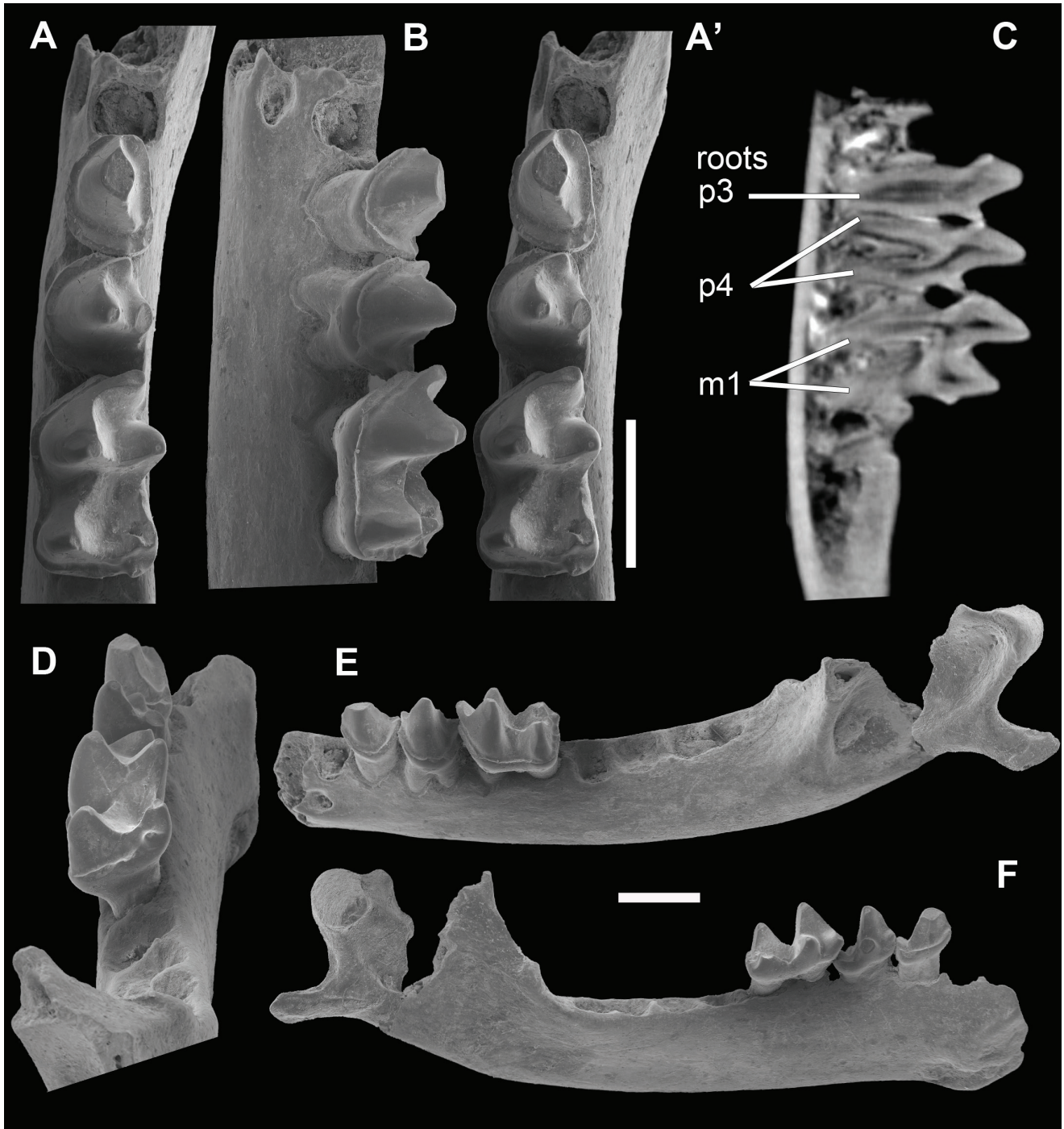


Figure 3. *Premonycteris vesper* gen. et sp. nov., Prémontré, Aisne, France; late Ypresian, Early Eocene. SLP 29 BS 193; partial left dentary with p3, p4 and m1, partial alveolus for c1, alveoli for p2, m2-3, and most of ascending ramus. **A-A'**, p3-m1, stereopair, occlusal view; **B**, buccal view; **C**, microCT axial section showing roots of p3-m1; **D**, posterior view; **E**, dentary, buccal view; **F**, dentary, lingual view. Scale bars = 1 mm.

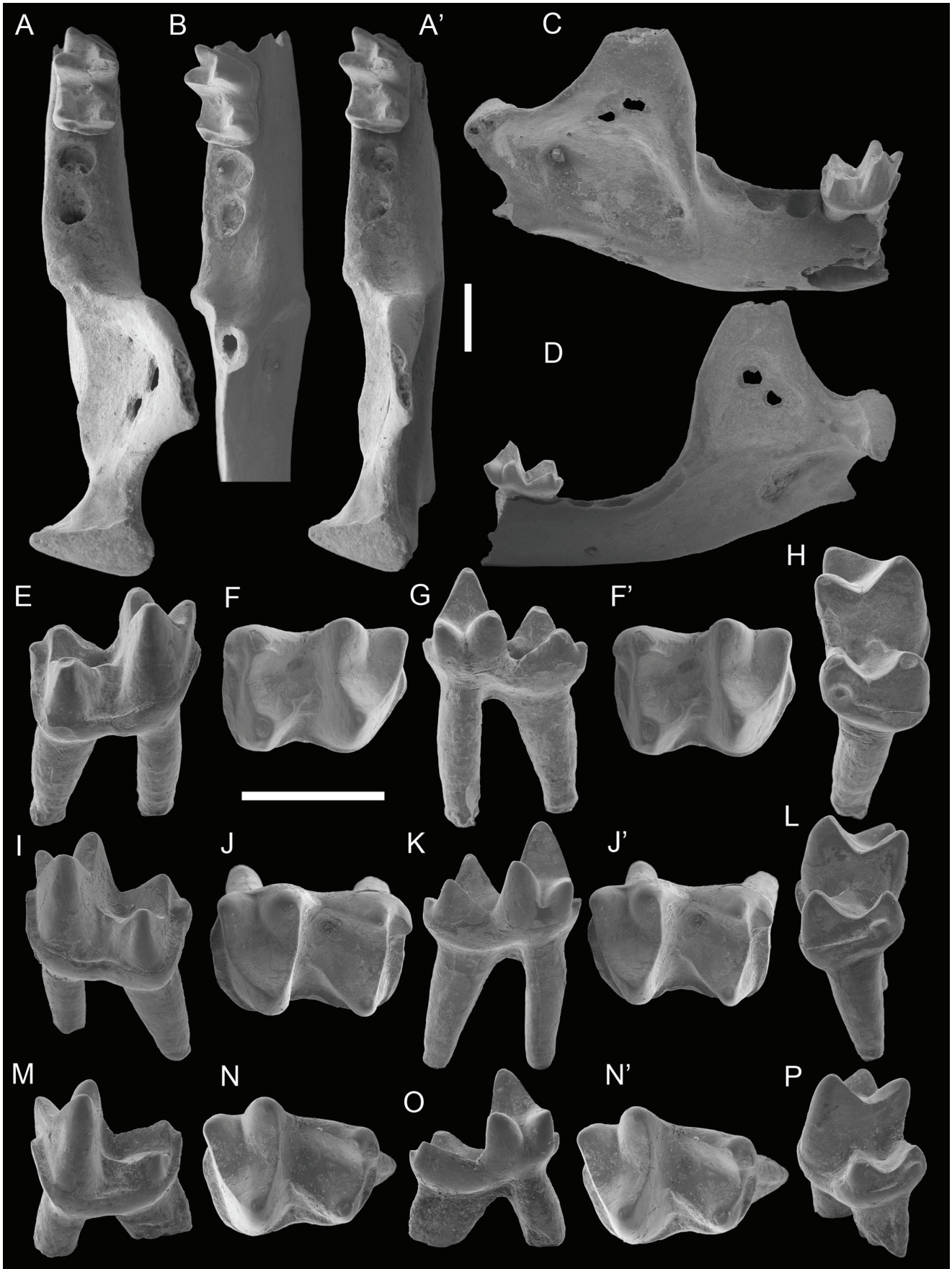


Figure 4. *Premonycteris vesper* gen. et sp. nov. SLP 29 PE 875, right dentary fragment with m2 and ascending ramus. A-A', stereopair, occlusal view; C, buccal view; D, lingual view. SLP 29 PE 614, right dentary fragment with m2. B, oblique-occlusal view. SLP 27 PR 8, right m2; E, buccal view; F-F', stereopair, occlusal view; G, lingual view; H, posterior view. PL PRE 611, left m2; I, buccal view; J-J', stereopair, occlusal view; K, lingual view; L, posterior view. SLP 29 PE 369, left m3; M, buccal view; N-N', stereopair, occlusal view; O, lingual view; P, posterior view. Scale bars = 1 mm.

familial assignment of *Lapichiropteryx* and *Stehlinia* species has been questioned by Smith *et al.* (2012), who noted that they share, among other features, a short p4 not found in other palaeochiropterygids (see below).

Irrespective, none of the archaic Eocene bats, including *Lapichiropteryx* and *Stehlinia* species, have a single-rooted p3, nor do they have myotodont lower molars (although the structure is not clear in *Onychonycteris finneyi*; Gunnell *et al.*, 2011). It is the combined presence of these features that persuades us *Premonycteris* does not belong in any of the extinct bat families.

In the myotodont lower molar structure of bats, the posteristid directly joins the hypoconid to the entoconid, and the posterolingual hypoconulid is typically greatly reduced with respect to the entoconid and isolated or linked to it by a small crest (as defined by Menu & Sigé, 1971; Sigé *et al.*, 2012; Fig. 2). The posteristid forms a blade that cuts against the anterior face of the paracone in the following upper molar. Myotodonty is less common than nyctalodonty among bats and may be more evolutionarily derived than the other dental patterns (nyctalodonty and necromantodonty; Menu & Sigé, 1971; Fig. 2). Myotodonty appears to have been independently acquired several times in various families, for example, among molossids (e.g., Hand, 1990; Maitre, 2014), phyllostomids (e.g., Sigé *et al.*, 2012), mystacinids (Hand *et al.*, 1998) and myzopodids (Gunnell *et al.*, 2014), but most frequently among vespertilionids with the majority of species and genera showing this pattern (Menu & Sigé, 1971; Menu, 1985, 1987; and see below). Several authors have noted that the pattern can be variable in some populations of some species (see examples in Sigé, 1995; Maitre, 2014); an intermediate structure, submyotodonty, is also recognized, in which the posteristid connects the hypoconid and entoconid as in myotodonty but a short crest may also connect the posteristid and hypoconulid (Legendre, 1984; Fig. 2). Generally, however, one pattern (nyctalodonty or myotodonty) dominates in a bat population (Menu & Sigé, 1971).

The combination of lower premolar and molar features noted above for *Premonycteris vesper* distinguishes it not only from extinct Eocene bat families but also from two of the four modern bat superfamilies, Rhinolophoidea and Emballonuroidea (Table 2). Rhinolophoids are characterized by p3 absent or tiny, relatively long p4 lacking metaconid, and presence of nyctalodont molars. Emballonurooids typically have two

lower premolars (except Eocene *Tachypteron* which retains a two-rooted p3; Table 2) and nyctalodont molars (although myotodonty is observed in some *Vespertiliavus* populations; Sigé, 1995; Maitre, 2014).

Noctilionoids exhibit other combinations of these features (see Differential diagnosis and Table 2). Myzopodids have three lower premolars and myotodont molars but reduced p3 and p4 without metaconid. Mormoopids have three lower premolars and myotodont molars but p3 either small and single-rooted or large and double-rooted. Noctilionids and mystacinids have myotodont molars but only two lower premolars. Phyllostomids have two or three lower premolars but generally a p4 lacking metaconid and nyctalodont molars (or modified for fruit, nectar or blood feeding). Thyropterids have myotodont molars and three premolars but p3 has two roots. Furipterids and extinct speonycterids have three premolars but nyctalodont lower molars. Thyropterids, furipterids and mormoopids (*Mormoops* spp.), like natalids and kerivoulines (below), differ additionally in having a low coronoid process of the dentary that is level with the condyloid process, reflecting significant dorsal cranial flexion (Morgan & Czaplewski, 2003) evidently not present in *Premonycteris vesper*.

The remaining, most speciose modern bat superfamily, Vespertilionoidea, contains the families Vespertilionidae (~400 spp.), Miniopteridae (20 spp.), Cistugidae (2 spp.), Natalidae (11 spp.), Molossidae (~100 spp.) and extinct Philisidae (6 spp.) (Simmons, 2005a; Lack *et al.*, 2010; Ravel *et al.*, 2015). Molossids retain only two lower premolars, both with two roots, and generally have nyctalodont but sometimes myotodont lower molars (Table 2). Philisids have myotodont molars but only two lower premolars (premolars unknown in *Dizzya*). Three lower premolars occur in natalids and miniopterids, but natalids have a two-rooted p3 and nyctalodont molars, while miniopterids have a single-rooted p3 but nyctalodont molars. Only (some) vespertilionids have three lower premolars, a single-rooted p3, short p4, and myotodont lower molars (e.g., species of *Myotis*, *Kerivoula*, *Plecotus*, *Idionycteris*; Table 2 and see below). The morphology of the dentary of *Premonycteris* (see Description above and Figs 3-4) is also consistent with that found in most vespertilionids (except kerivoulines as noted above).

Molecular and morphological data indicate that Vespertilionidae is monophyletic (e.g., Simmons *et al.*, 2008; Lack *et al.*, 2010) but no unambiguous dental synapomorphies for the family have been identified (Simmons & Geisler, 1998; Czaplewski & Morgan, 2001; Horáček, 2001; Hofer & Van den Bussche, 2003; Eick *et al.*, 2005; Gunnell & Simmons, 2005; Simmons *et al.*, 2008; Ravel *et al.*, 2015). Vespertilionids are often characterized by their relatively unspecialized dentitions (e.g., Sigé, 1974; Menu, 1987; Horáček, 2001; Horáček *et al.*, 2006; Maitre, 2014). Slaughter (1970) noted that each dental feature considered primitive for bats can be found in some vespertilionid, although no modern species retains them all. Submyotodonty has been suggested as the plesiomorphic dental pattern among vespertilionoids (e.g., Ravel *et al.*, 2015), and myotodonty probably the primitive condition in vespertilionids (e.g., Sigé, 1985; Horáček, 2001; Gunnell *et al.*, 2012), but a thorough phylogenetic analysis of this speciose family is needed to formally establish this. In their molecular analysis of myotines, Lack *et al.* (2010) note that few informative taxonomic characters, extensive morphological convergence, and a likely rapid initial diversification have made it difficult to unravel the evolutionary relationships of vespertilionids on the basis of morphology.

Nevertheless, the combination of three lower premolars, a

Specimen no.	Position	Length	Width	Trig. width	Tal. width
SLP 29 BS 193*	p3-m1				
	p3	0.75	0.70		
	p4	0.75	0.80		
	m1	1.35		0.95	0.90
SLP 29 PE 110	m1	1.40		0.90	0.95
PRE 273	m1	1.40		0.90 (est.)	0.95
PRE 347	?m1	1.40		1.00	0.90
PRE 764	m1	1.35		1.00	1.00
PL PRE 1076	m1	1.35		0.95	0.90
SLP 29 PE 875*	m2	1.30		0.90	0.90
SLP 29 PE 614*	m2	1.35		1.00	0.95
PRE 1136	?m2	1.40		0.95	0.95
PRE 611*	m2	1.45		1.00	1.00
SLP 27 PR 8*	m2	1.40		0.90	0.85
SLP 43 PR 17	m2	1.35		0.90	0.90
SLP 29 PE 369*	m3	1.30		0.90	0.75
SLP 29 PE 290	m3	1.30		0.95	0.70

Table 1. Measurements (mm) of specimens of *Premonycteris vesper* gen. et sp. nov. Abbreviations: Trig., trigonid; Tal., talonid; *, figured; est., estimate.

single-rooted p3, short p4 with metaconid, myotodont lower molars, as well as tall coronoid process of the dentary, is most similar to features frequently seen among vespertilionids (see below), and not other bat families, which is why, on the basis of available data, we refer *Premonycteris vesper* to Vespertilionidae. We recognise, however, that these features almost certainly represent a mosaic of plesiomorphic and apomorphic traits, and that it is possible, when more of the vespertilionoid fossil record is known, and/or dental synapomorphies for vespertilionids identified, that

Premonycteris vesper may be recognized as a derived member of a stem group rather than an early representative of the modern clade.

While *Premonycteris vesper* is interpreted here to be a vespertilionid for the reasons noted above, it is not clear to which, if any, of the currently recognized four vespertilionid subfamilies (sensu Roehrs *et al.*, 2010) it might belong. A member of the extant myotine subfamily, *Khonsunycteris aegypticus* from the late Eocene (~34 Ma) of the Fayum, Egypt, is the oldest, widely accepted fossil record for Vespertilionidae

Family	Species	Epoch	FAD (Ma)	Lower premolars	Lower premolar size	p3 roots	p4 metaconid	Molar form
Extinct Eocene families								
Onychonycteridae†	<i>Onychonycteris finneyi</i>	Early Eocene	53	3	p4>p3<p2	2	absent	myotodont?
	<i>Eppsinycteris anglica</i>	Early Eocene	55	3	p4>=p3	3	present	necromantodont
	<i>Honrovits tsuwape</i>	Early Eocene	53	3	p4>p3<p2	2	absent	necromantodont
Icaronycteridae†	<i>Icaronycteris menui</i>	Early Eocene	54	3	p4>p3>p2	2	present	nyctalodont
Archaeonycteridae†	<i>Archaeonycteris</i> spp.	E-M Eocene	55	3	p4>p3>p2	2	present	necromantodont
	<i>Protonycteris gunnelli</i>	Early Eocene	54	3	p4>p3>p2	2	present	necromantodont
Hassianycteridae†	<i>Hassianycteris</i> spp.	E-M Eocene	54	3	p4>=p3>p2	2	absent	nyctalodont
Palaeochiropterygidae†	<i>Palaeochiropteryx</i> spp.	Middle Eocene	47	3	p4>p3>p2	2	present	nyctalodont
?Palaeochiropterygidae†	<i>Stehlinia</i> spp.	M Eoc-E Oligo	43	3	p4>=p3>p2	2	variable	nyctalodont
	<i>Lapichiropteryx xiei</i>	Middle Eocene		3	p4>=p3>p2	2	present	nyctalodont
Family indet.†	<i>Necromantis adichaster</i>	Middle Eocene	43	3	p4= p2>p3	1	absent	necromantodont
Mixopterygidae†		M Eoc - L Oligo		2	p4>p2	-	?absent	nyctalodont
	<i>Carcinopteryx maximinensis</i>	M Eocene	43	2	p4>p2	-	?absent	nyctalodont
SF Emballonuroidea		E Eocene-Recent		2-3		-		nyctalodont
Emballonuridae	<i>Tachypteron franzeni</i> †	M Eocene	47	3	p4>p3>p2	2	?absent	nyctalodont
	<i>Vespertiliavus</i> spp. †	M Eoc - L Oligo	43	2	p4=p2	-	present	nyctalodont (var)
SF Rhinolophoidea		E Eocene-Recent		2-3				nyctalodont
Rhinolophidae	<i>Protorhinolophus shanghuangensis</i> †	M Eocene	43	3	p4>p3<p2	1	absent	nyctalodont
Hipposideridae	<i>Hipposideros schlosseri</i> †	M Eocene	43	2	p4>p2	-	absent	nyctalodont
Megadermatidae	<i>Saharaderma pseudovampyrus</i> †	L Eocene	34	2	p4>p2	-	absent	nyctalodont
SF Noctilionoidea		L Eocene-Recent		2-3				myot & nyctalodont
Myzopodidae	<i>Phasmatonycteris</i> spp. †	L Eoc-L Oligo	37.5	3	p4>p3<p2	1	absent	myotodont
Speonycteridae†	<i>Speonycteris aurantiadens</i>	E Oligocene	30	3	p4>p3<p2	2	?present	nyctalodont
Mystacinidae	<i>Icarops paradox</i> †	E Miocene	18	2	p4>p2	-	unknown	myotodont
Mormoopidae	Mormoopid indet.	E Oligocene	30	3	p4>p3=p2	2	absent	nyctalodont
	<i>Pteronotus</i> spp.	Pleist-Recent	2	3	p4>p3<p2	1	absent	myotodont
	<i>Mormoops</i> spp.	Pleist-Recent	2	3	p4=p3=p2	2	absent	nyctalodont
Noctilionidae	<i>Noctilio</i> spp.	M Miocene	13	2	p4>p2	-	absent	myotodont
Phyllostomidae	<i>Macrotis waterhousii</i>	Pleist-Recent	2	3	p4=p3=p2	2	absent	myotodont
	<i>Chrotopterus</i> spp.	Pleist-Recent	2	3	p4>p3<p2	1	?absent	nyctalodont
	<i>Notonycteris</i> spp. †	M Miocene	13	3	p4>p3<p2	1	unknown	nyctalodont
SF Vespertilionoidea		E Eocene-Recent		2-3				myot & nyctalodont
Natalidae		L Oligo-Recent						
	<i>Natalus</i> spp.	Pliocene-Recent	5	3	p4=p3=p2	2	absent	nyctalodont
	<i>Primonatalus prattae</i> †	E Miocene	19	3	p4=p3>p2	2	?unknown	nyctalodont
Molossidae		L Eocene-Recent		2				myot & nyctalodont
	<i>Cuvierimops</i> spp. †	L Eoc-L Oligo	37	2	p4>p2	-	present	myot & nyctalodont
Miniopteridae	<i>Miniopterus</i> spp.	E Mioc-Recent	22	3	p4>p3>=p2	2	absent	nyctalodont
Philisidae†		E Eocene-E Oligo		2				myotodont
	<i>Dizya exsultans</i>	Early Eocene	50	unknown	unknown	?	unknown	myotodont
	<i>Witwata schlosseri</i>	Late Eocene	37.5	2	p4=p3	-	?present	myotodont
Cistugidae	<i>Cistugo</i> spp.	Recent	0.1	3	p4 >p3<p2	1	?absent	myotodont
Vespertilionidae	<i>Premonycteris vesper</i> †	Early Eocene	50	3	p4=p3>p2	1	present	myotodont
	<i>Khonsunycteris aegyptiacus</i> †	Late Eocene	34	3	p4 >p3<p2	2	absent	myotodont
	<i>Quinetia misoniei</i> †	E Oligocene	32.4	3	p4 >p3=>p2	1	unknown	nyctalodont
	<i>Hanakia fejfari</i> †	E Oligocene	32.4	3	p4>p3<p2	1	absent	myotodont
	<i>Myotis/Leucone</i> spp.	E Oligo-Recent	31	3	p4 >p3<p2	1	absent	myotodont
	<i>Murina</i> spp.	Pliocene-Recent	5	2	p4>p3	-	present	nyctalodont
	<i>Kerivoula</i> spp.	Pliocene-Recent	5	3	p4=p3=p2	1	absent	myotodont
	<i>Idionycteris phyllotis</i>	Recent	0.1	3	p4>p3<p2	1	present	myotodont
	<i>Plecotus</i> spp.	M Mio-Recent	9	3	p4>p3<=p2	1	variable	myotodont
	<i>Lasionycteris</i> spp.	Pliocene-Recent	5	3	p4>p3=p2	1	?absent	nyctalodont
	<i>Nyctalus</i> spp.	L Oligo-Recent	32.4	2	p4=p2	-	absent	nyctalodont
	<i>Pipistrellus</i> spp.	L Mio-Recent	10	2	p4=p2	-	variable	myot & nyctalodont

Table 2. Summary of dental features for representative bat taxa noted in text. Abbreviations: FAD, first appearance date ; E, early; Eoc, Eocene; L, late; M, middle; Ma, millions of years ago; Mio, Miocene; myot, myotodont; Oligo, Oligocene; †, extinct taxon; SF, superfamily. Data from Czaplewski & Morgan, 2001, 2012; Eiting & Gunnell, 2009; Gunnell *et al.*, 2008, 2014; Gunnell & Simmons, 2005; Harrison & Hooker, 2010; Hooker, 1996; Horáček, 2001; Maitre, 2014; Morgan & Czaplewski, 2003, 2012; Ravel *et al.*, 2011, 2012, 2014, 2015; Sigé, 1991; Smith *et al.*, 2012; Storch *et al.*, 2002; and pers. obs. (S. J. Hand, 2016).

(Gunnell *et al.*, 2008; Figs 5-6). *Premonycteris vesper* shares with extant myotines and *Khonsunycteris aegypticus* presence of three premolars and myotodont lower molars, but differs in its taller and longer, but narrower p3 and shorter p4 with metaconid. It differs additionally from *K. aegypticus* in p3 having one root, and an evidently less reduced m3 (known only by alveoli in *Khonsunycteris*). Kerivoulines, like *Premonycteris vesper*, have three lower premolars and myotodont molars, but p2 is larger, p3 double-rooted, p4 lacks a metaconid and the coronoid process of the dentary is relatively low with respect to the condyle. Murinines have two lower premolars and generally nyctalodont lower molars, and are least similar to *Premonycteris vesper*. In vespertilionines with three premolars and myotodont molars (e.g., *Plecotus*, *Idionycteris* and allies; Table 2), p2 and p3 are usually conspicuously smaller than p4, with p3 often smallest. Overall, the mosaic of traits observed in the lower dentition of *Premonycteris vesper* does not precisely match any modern vespertilionid subfamily, but could be ancestral to vespertilionines. Until the upper dentition of *Premonycteris* is known, we refrain from assigning it to an existing modern vespertilionid subfamily.

Premonycteris vesper extends the fossil record of the family Vespertilionidae back to 50 Ma (Fig. 5). This late Early Eocene age is similar to the oldest record for the modern bat families Hipposideridae and Emballonuridae, undescribed taxa from the late Early Eocene of Chambi, Tunisia (Sigé, 1991; Ravel *et al.*, 2011, 2014, 2015; Figs 5-6), and only 5 million years younger than the oldest currently known record for Chiroptera: *Archaeonycteris praecursor* from Silveirinha, Portugal (Tabuce *et al.*, 2009; Figs 5-6). Globally, Early Eocene bat faunas are characterized by species referred to several extinct families (see Smith *et al.*, 2012 for a review of taxa) that apparently represent stem taxa forming progressively closer sister-groups to the modern bat clade (e.g., Simmons & Geisler,

1998; Gunnell & Simmons, 2005; Simmons *et al.*, 2008). Alternatively, some could represent a separate archaic clade (O’Leary *et al.*, 2013). During the Middle Eocene, there was a decline of archaic bat families and increasing representation of modern families in Eurasia, Africa and North America (i.e., where the record is sufficiently known; Fig. 5). At Prémontré, the vespertilionid *Premonycteris vesper* lived alongside at least two archaic bat species (*Icaronycteris* sp. indet. and cf. *Archaeonycteris*; Dégrémont *et al.*, 1985, and pers. obs. [S. J. Hand, 2016]).

Discovery of *Premonycteris vesper* in the late Early Eocene of northern France adds complexity to the evolutionary history of vespertilionoids. The presence of modern bat groups in the late Early Eocene of Afro-Arabia, and their abrupt, taxonomically-diverse appearance in Middle Eocene Europe, has suggested an African source for the group with subsequent immigration into Europe (Sigé, 1991; Gunnell *et al.*, 2008; Ravel *et al.*, 2011, 2015). The extinct philisids of Paleogene Afro-Arabia have been identified as an early vespertilionid offshoot, and the Late Eocene *Khonsunycteris aegypticus* as an ancestor for crown vespertilionids (Ravel *et al.*, 2015: fig. 6). *Premonycteris vesper* appears to be equally or more derived in some features (myotodont lower molars, p3 single rooted) than the younger myotine vespertilionid *Khonsunycteris* but less derived in other features (larger p3, molariform p4), suggesting these two Eocene vespertilionids shared an earlier common ancestor. Further, Afro-Arabian philisids appear to be more derived than the similarly-aged European *Premonycteris vesper* in at least some dental features (two lower premolars, m3 lacking hypoconulid). Taken together, these observations suggest that an African origin for superfamily Vespertilionoidea is less certain.

Molecular estimates for the time of divergence of vespertilionids from other vespertilionoids (i.e., natalids,

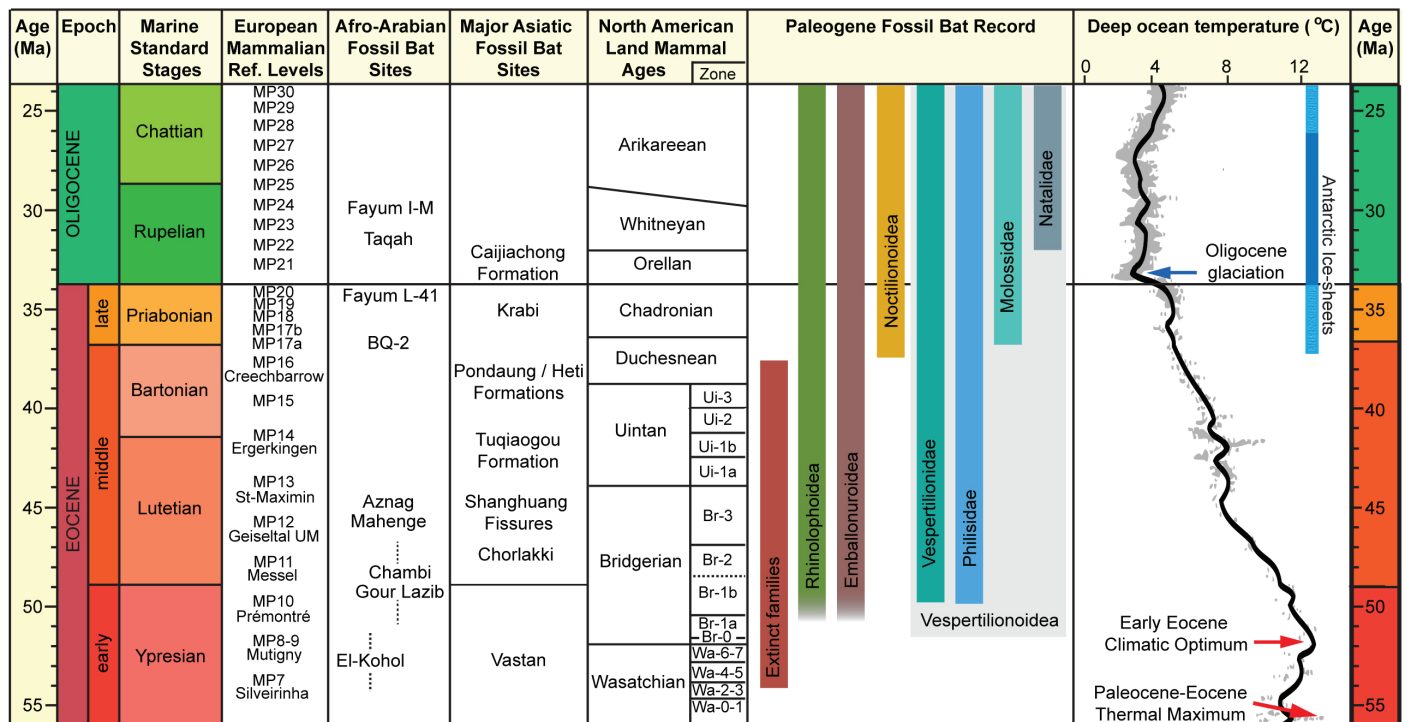


Figure 5. Correlation chart of the Paleogene fossil bat record with marine standard stages, European Mammalian Paleogene (MP) Reference Levels, North American Land Mammal Ages, European, Afro-Arabian and Asiatic fossil bat sites and Paleogene climate change. Modified from Godinot (2014). Deep ocean temperatures modified from Zachos *et al.* (2001).

miniopterids, molossids, cistugids) range from 55 to 30 Ma (e.g., Teeling *et al.*, 2005 [53–42 Ma]; Eick *et al.*, 2005 [49–41 Ma]; Miller-Butterworth *et al.*, 2007 [49–38 Ma]; Meredith *et al.*, 2011 [52–42 Ma]; Lack *et al.*, 2010 [38–30 Ma]; Yu *et al.*, 2014 [55–51 Ma]). Fossils used to calibrate the molecular clock for vespertilionoid evolution, and bats more broadly, include the early Middle Eocene appearance of *Stehlinia* spp. and the late Middle Eocene *Wallia scalopidens* (e.g., Teeling *et al.*, 2005; Miller-Butterworth *et al.*, 2007; Meredith *et al.*, 2011; O’Leary *et al.*, 2013). Use of these calibration points leads to a minimum date of 37 Ma (end of Middle Eocene) for the split between vespertilionids and molossids. As noted above, the familial identity of *Stehlinia* species among bats remains uncertain (e.g., Smith *et al.*, 2012) and *Wallia*, originally described as a non-bat (lipotyphlan) by Storer (1984) and interpreted as a possible molossid by Legendre (1985), is currently regarded as a non-chiropteran mammal (Smith *et al.*, 2012). Nevertheless, widely accepted molossids (*Cuvierimops* spp.) do appear in the early Late Eocene record (Maitre, 2014), and 37 Ma is a reasonable *minimum* date for this divergence. If we are correct in our assignment of *Premonycteris vesper* to Vespertilionidae, this fossil provides a new calibration point for the family, and crown Vespertionoidea more broadly, in dated molecular phylogenies of bats. At 50 Ma, *Premonycteris* is similar in age or older than the time of vespertilionid origins predicted by analyses of genomic data.

The fossil record for vespertilionoids, despite evidently being only ~25% complete, is better than that for most bat superfamilies (Eiting & Gunnell, 2009). Vespertilionid generic diversity is lowest in the Paleogene (5 genera), increasing to 10 – 20 genera after the early Miocene, and highest at 51 genera today (Eiting & Gunnell, 2009; Simmons, 2005b; pers. comm. N. Simmons, 2016). Molecular analyses detect an increase in diversity at the end of the Eocene, as well as a Miocene explosion of vespertilionid lineages (e.g., Jones *et al.*, 2005; Stadelman *et al.*, 2007; Lack *et al.*, 2010; Yu *et al.*, 2014). These authors suggest that these diversifications probably relate to global cooling at the end of the Eocene (Fig. 5) and the later Miocene, with lower sea levels and new land connections emerging, as well as the decline of non-hibernating rhinolophoid and emballonuroid bats in temperate



Figure 6. Eocene fossil bat localities noted in text and Fig. 5 (modified from Smith *et al.*, 2012: figs 16 & 17); palaeogeographic reconstruction of 50 Ma after Scotese (2006). Filled circle, Early Eocene; open circle, Middle Eocene; open triangle, Middle-Late Eocene; filled triangle, Middle Eocene-Oligocene site.

zones. These events would have provided new opportunities for vespertilionids able to exploit energy-conserving metabolic and behavioural capabilities, such as torpor, migration and delayed fertilization, to cope with increasingly unpredictable conditions and resources (e.g., Horáček, 2001; Stadelman *et al.*, 2007; Lack *et al.*, 2010; Yu *et al.*, 2014).

With an estimated weight of 9.5 g (see Description above), *Premonycteris vesper* was a relatively small bat, compared with an average 13.8 g for 905 extant bat species, and 3 to 50 g for living vespers (Smith *et al.*, 2004; Gunnell *et al.*, 2009). It was significantly smaller than many Early Eocene bats (e.g., 24 – 41 g for *Icaronycteris*, *Onychonycteris* and *Archaeonycteris* spp.; Giannini *et al.*, 2012) but similar to estimates for the Middle Eocene Messel palaeochiropterygid *Palaeochiropteryx tupaiodon* (Giannini *et al.*, 2012), and larger than the early-middle Early Eocene palaeochiropterygid *Microchiropteryx foliae* from Vastan, India (Smith *et al.*, 2007: table 1 dental measurements; Rose *et al.*, 2014; Smith *et al.*, 2015).

Premonycteris lived during the Early Eocene Climatic Optimum (EEOC) when the climate was globally warmer than today (53–50 Ma; Fig. 5), with an estimated mean annual sea surface temperature 50 Ma in the Paris Basin of ~22°C (Huyghe *et al.*, 2015). Warm, humid megathermal rainforest extended to high latitudes in the EEOC and this was associated with high diversification rates among mammals (Collinson, 2000). In the Prémontre assemblage, the abundant remains of primates, arboreal rodents and bats, and a rarity of large mammals, suggest a locally densely forested habitat (Dégrémont *et al.*, 1985). There is no evidence of regional karst or caves and the evidence collectively suggests *Premonycteris* was probably a tree-dweller like many extant vespertilionids (e.g., *Lasiurus* and *Pipistrellus* species; Menzel *et al.*, 1998; Veilleux *et al.*, 2003). Its simple dilambdodont dentition indicates that *Premonycteris* ate insects, perhaps caught by aerial hawking or gleaning like many vespertilionids past and present (Norberg & Rayner, 1987; Norberg, 1989; Horáček, 2001), and differs significantly from the specialized dentition and proposed carnivorous diet of contemporary philisids (Ravel *et al.*, 2015). Simmons & Geisler (1998) have argued that continuous aerial hawking using echolocation was the primitive foraging strategy for crown group bats, and a key innovation in their evolution.

In conclusion, we remain in the dark about whether *Premonycteris*, Europe’s oldest vespertilionid, was an immigrant or evolved in situ during the EEOC from one of the extinct groups such as palaeochiropterygids. *Premonycteris* is still poorly known but does not appear to be a member of any modern vespertilionid subfamily. As noted above, it is also possible that *Premonycteris vesper* may be a derived member of a stem group rather than an early representative of the modern clade Vespertilionidae. Much of the fossil record, phylogenetic relationships and evolutionary history of today’s most successful family of bats remains to be revealed.

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BIBLIOGRAPHY

- Adnet, S., Cappetta, H., 2008. New fossil triakid sharks from the early Eocene of Prémontre, France, and comments on fossil record of the family. *Acta Palaeontologica Polonica* 53, 433-448. doi: [10.4202/app.2008.0306](https://doi.org/10.4202/app.2008.0306)
- Aubry, M.-P., Thiry, M., Dupuis, C., Berggren, W., 2005. The Sparnacian deposits of the Paris Basin: a lithostratigraphic classification. *Stratigraphy* 2, 65-100.
- Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D., Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L., Purvis, A., 2007. The delayed rise of present-day mammals. *Nature* 446, 507-512. doi:[10.1038/nature05634](https://doi.org/10.1038/nature05634)
- Cappetta, H., 1992. Carcharhiniformes nouveaux (Chondrichthyes, Neoselachii) de l'Yprésien du Bassin de Paris. *Geobios* 25, 639-646.
- Collinson, M. E., 2000. Cenozoic evolution of modern plant communities and vegetation. In: Culver, S. J., Rawson, P. F. (Eds.), *Biotic Response to Global Change*. Cambridge University Press, Cambridge, pp. 223-243.
- Czaplewski, N. J., G. S. Morgan., 2001. A new vespertilionid bat (Mammalia: Chiroptera) from the Early Miocene (Hemingfordian) of Florida. *Journal of Vertebrate Paleontology* 20, 736-742.
- Czaplewski, N. J., Morgan, G. S., 2012. New basal noctilionoid bats (Mammalia: Chiroptera) from the Oligocene of subtropical North America. In: Gunnell, G. F., Simmons, N. B. (Eds.), *Evolutionary History of Bats*. Cambridge University Press, Boston, pp. 162-209.
- Dégrémont, E., Duchaussois, F., Hautefeuille, F., Laurain, P., Louis, P., Tetu, R., 1985. Paléontologie: découverte d'un gisement du Cuisien tardif à Prémontre (Aisne). *Bulletin d'Information des Géologues du Bassin de Paris* 22, 11-18.
- Eick, G. N., Jacobs, D. S., Matthee, C. A., 2005. A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (Chiroptera). *Molecular Biology and Evolution* 22, 1869-1886.
- Eiting, T. P., Gunnell, G. F., 2009. Global completeness of the bat fossil record. *Journal of Mammalian Evolution* 16, 151-173. doi: [10.1007/s10914-009-9118-x](https://doi.org/10.1007/s10914-009-9118-x)
- Escarguel, G., 1999. Les rongeurs de l'Eocène inférieur et moyen d'Europe occidentale: systématique, phylogénie, biochronologie et paléobiogéographie des niveaux-repères MP 7 à MP 14. *Palaeovertebrata* 28, 89-351.
- Giannini, N. P., Gunnell, G. F., Habersetzer, J., Simmons, N. B., 2012. Early evolution of body size. In: Gunnell, G. F., Simmons, N. B., (Eds.), *Evolutionary History of Bats Fossils, Molecules and Morphology*. Cambridge University Press, Boston, pp. 530-555.
- Godinot, M., 2014. Fossil record of the Primates from the Paleocene to the Oligocene. In: Henke, W., Tattersal, I. (Ed.), *Handbook of Paleoanthropology*. Springer-Verlag, Berlin, pp. 1-102.
- Godinot, M., Russell, D. E., Louis, P., 1992. Oldest known *Nannopithecus* (Primates, Omomyiformes) from the early Eocene of France. *Folia Primatologica* 58, 32-40.
- Gunnell, G. F., Simmons, N. B., 2005. Fossil evidence and the origin of bats. *Journal of Mammalian Evolution* 12, 209-246.
- Gunnell, G. F., Simons, E. L., Seiffert, E. R., 2008. New bats (Mammalia: Chiroptera) from the late Eocene and early Oligocene, Fayum Depression, Egypt. *Journal of Vertebrate Paleontology* 28, 1-11.
- Gunnell, G. F., Eiting, T. P., Simons, E. L., 2012. African Vespertilionoidea (Chiroptera) and the antiquity of Myotinae. In: Gunnell, G. F., Simmons, N. B. (Eds.) *Evolutionary History of Bats: Fossils, Molecules and Morphology*. Cambridge University Press, Boston, pp. 252-266.
- Gunnell, G. F., Worsham, S. R., Seiffert, E. R., Simons, E. L., 2009. *Vampyravus orientalis* Schlosser (Chiroptera) from the early Oligocene of Egypt – body mass, humeral morphology and affinities. *Acta Chiropterologica* 11, 271-278.
- Gunnell, G. F., Simmons, N. B., Seiffert, E. R., 2014. New Myzopodidae (Chiroptera) from the Late Paleogene of Egypt: emended family diagnosis and biogeographic origins of Noctilionoidea. *PLoS ONE* 9(2): e86712. doi: [10.1371/journal.pone.0086712](https://doi.org/10.1371/journal.pone.0086712)
- Gunnell, G. F., Habersetzer, J., Schlosser-Sturm, E., Simmons, N. B., Smith, T., 2011. Primitive chiropteran teeth: the complete dentition of the Messel bat *Archaeonycteris trigonodon*. In: Lehmann, T., Schaal, S. F. K. (Eds.), *The World at the Time of Messel*. HC Volker Mosbrugger, Senckenberg Research Institute and Natural History Museum, Frankfurt, pp. 73-76.
- Habersetzer, J., Storch, G., 1987. Klassifikation und funktionelle Flügelmorphologie paläogener Fledermäuse (Mammalia, Chiroptera). *Courier Forschungsinstitut Senckenberg* 91, 117-150.
- Habersetzer, J., Richter, G., Storch, G., 1994. Paleocology of early middle Eocene bats from Messel, FRG. *Aspects of flight, feeding and echolocation*. *Historical Biology* 8, 235-260.
- Hand, S.J., 1990. First Tertiary molossid (Microchiroptera: Molossidae) from Australia: its phylogenetic and biogeographic implications. *Memoirs of the Queensland Museum* 28, 175-192.
- Hand, S.J., Sigé, B., Maitre, E., 2012. *Necromantis* Weithofer, 1887, large carnivorous Middle and Late Eocene bats from the French Quercy Phosphorites: new data and unresolved relationships. In: Gunnell, G. F., Simmons, N. B. (Eds.) *Evolutionary History of Bats: Fossils, Molecules and Morphology*. Cambridge University Press, Boston, pp. 210-251.
- Hand, S. J., Novacek, M., Godthelp, H., Archer, M., 1994. First Eocene bat from Australia. *Journal of Vertebrate Paleontology* 14, 375-381.
- Hand, S.J., Murray, P.F., Megirian, D., Archer, M., Godthelp, H., 1998. Mystacinid bats (Microchiroptera) from the Australian Tertiary. *Journal of Paleontology* 72, 538-545.
- Hand, S. J., Sigé, B., Archer, M., Gunnell, G. F., Simmons, N. B., 2015. A new early Eocene (Ypresian) bat from Pourcy, Paris Basin, France, with comments on patterns of diversity in the earliest chiropterans. *Journal of Mammalian Evolution* 22, 343-354. doi: [10.1007/s10914-015-9286-9](https://doi.org/10.1007/s10914-015-9286-9)
- Harrison D. L., Hooker, J. J., 2010. Late middle Eocene bats from the Creechbarrow Limestone Formation, Dorset, south England with description of a new species of *Archaeonycteris* (Chiroptera: Archaeonycteridae). *Acta Chiropterologica* 12, 1-18.
- Hooper, S. R., Van Den Bussche, R. A., 2003. Molecular phylogenetics of the chiropteran family Vespertilionidae. *Acta Chiropterologica* 5, 1-63.
- Hooker, J. J., 1996. A primitive emballonurid bat (Chiroptera, Mammalia) from the earliest Eocene of England. *Palaeovertebrata* 25, 287-300.
- Horáček, I., 2001. On the early history of vespertilionid bats in Europe: the Lower Miocene record from the Bohemian Massif. *Lynx* 32, 123-154.
- Horáček, I., Fejfar, O., Hulva, P., 2006. A new genus of vespertilionid bat from the Early Miocene of Jebel Zelten, Libya, with comments on *Scotophilus* and early history of vespertilionid bats (Chiroptera). *Lynx* 37, 131-150.
- Huyghe, D., Lartaud, F., Emmanuel, L., Merle, D., Renard, M., 2015. Palaeogene climate evolution in the Paris Basin from oxygen

- stable isotope ($d^{18}O$) compositions of marine molluscs. *Journal of the Geological Society* 172, 576-587. doi: [10.1144/jgs2015-016](https://doi.org/10.1144/jgs2015-016)
- Jones, K. E., Bininda-Emonds, O. R. P., Gittleman, J. L., 2005. Bats, clocks, and rocks: diversification patterns in Chiroptera. *Evolution* 59, 2243-2255.
- Lack, J. B., Roehrs, Z. P., Stanley, C. E., Ruedi, M., Van Den Bussche, R. A., 2010. Molecular phylogenetics of *Myotis* indicate familial-level divergence for the genus *Cistugo* (Chiroptera). *Journal of Mammalogy* 91, 976-992. doi: [10.1644/09-MAMM-A-192.1](https://doi.org/10.1644/09-MAMM-A-192.1)
- Lecomte, G., 1994. Étude paléontologique et sédimentologique de l'Yprésien de l'Est du Bassin de Paris. PhD, Université de Paris VI, Paris.
- Legendre, S., 1984. Étude odontologique des représentants actuels du groupe *Tadarida* (Chiroptera, Molossidae). Implications phylogéniques, systématiques et zoogéographiques. *Revue suisse de Zoologie* 91, 399-442.
- Legendre, S., 1985. Molossidés (Mammalia, Chiroptera) cénozoïques de l'Ancien et du Nouveau Monde : statut systématique; intégration phylogénique des données. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 170, 205-27.
- Louis, P., 1996. Recherches de mammifères paléogènes dans les départements de l'Ain et de la Marne pendant la deuxième moitié du vingtième siècle. *Palaeovertebrata* 25, 83-113.
- Maitre, E., 2014. Western European middle Eocene to lower Oligocene Chiroptera – systematics, phylogeny and palaeoecology based on new material from the Quercy (France). *Swiss Journal of Palaeontology* 133, 141-242.
- Marandat, B., 1991. Mammifères de l'Ilerdien moyen (Eocène inférieur) des Corbières et du Minervois (Bas-Languedoc, France). Systématique, biostratigraphie, corrélations. *Palaeovertebrata* 20, 55-144.
- Menu, H., 1985. Morphotypes dentaires actuels et fossiles des chiroptères Vespertilioninés. 1ère partie: étude des morphologies dentaires. *Palaeovertebrata* 15, 71-128.
- Menu, H., 1987. Morphotypes dentaires actuels et fossiles des chiroptères Vespertilioninés, 2ème partie: implications systématiques et phylogéniques. *Palaeovertebrata* 17, 77-150.
- Menu, H., Sigé, B., 1971. Nyctalodontie et myotodontie, importants caractères de grades évolutifs chez les chiroptères entomophages. *Comptes Rendus de l'Académie des Sciences Paris* 272, 1735-1738.
- Menzel, M. A., Carter, T. C., Chapman, B. R., Laerm, J., 1998. Quantitative comparison of tree roosts used by red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*). *Canadian Journal of Zoology* 76, 630-634.
- Meredith, R. W., Jane ka, J. E., Gatesy, J., Ryder, O. A., Fisher, C. A., Teeling, E. C., Goodbla, A., Eizirik, E., Simão, T. L. L., Stadler, T., Rabosky, D. L., Honeycutt, R. L., Flynn, J. J., Ingram, C. M., Steiner, C., Williams, T. L., Robinson, T. J., Burk-Herrick, A., Westerman, M., Ayoub, N. A., Springer, M. S., Murphy, W. J., 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334, 521-524. doi: [10.1126/science.1211028](https://doi.org/10.1126/science.1211028)
- Miller-Butterworth, C. M., Murphy, W. J., O'Brien, S. J., Jacobs, D. S., Springer, M. S., Teeling, E. C., 2007. A family matter: conclusive resolution of the taxonomic position of the long-fingered bats, *Miniopterus*. *Molecular Biology and Evolution* 24, 1553-1561.
- Morgan, G. S., Czaplewski, N. J., 2003. A new bat (Chiroptera: Natalidae) from the Early Miocene of Florida, with comments on natalid phylogeny. *Journal of Mammalogy* 84, 729-752.
- Morgan, G. S., Czaplewski, N. J., 2012. Evolutionary history of the Neotropical Chiroptera: the fossil record. In: Gunnell, G. F., Simmons, N. B., (Eds.), *Evolutionary History of Bats: Fossils, Molecules and Morphology*. Cambridge University Press, Boston, pp. 105-161.
- Norberg, U. M., 1989. Ecological determinates of bat wing shape and echolocation call structure with implications for some fossil bats. In: Hanák, V., Horáček, I., Gaisler, J. (Eds.), *European Bat Research 1987*. Charles University Press, Prague, pp. 197-211.
- Norberg, U. M., Rayner, J. M., 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society B* 316, 335-427.
- O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T. J., Giallombardo, A., Giannini, N. P., Goldberg, S. L., Kraatz, B. P., Luo, Z.-X., Meng, J., Ni, X., Novacek, M. J., Perini, F.A., Randall, Z. S., Rougier, G. W., Sargis, E. J., Silcox, M. T., Simmons, N. B., Spaulding, M., Velazco, P. M., Weksler, M., Wible, J. R., Cirranello, A. L., 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. *Science* 339, 662-667. doi: [10.1126/science.1229237](https://doi.org/10.1126/science.1229237)
- Ravel, A., Marivaux, L., Tabuce, R., Adaci, M., Mahboubi, M., Mebrouk, F., Bensalah, M., 2011. The oldest African bat from the early Eocene of El Kohol (Algeria). *Naturwissenschaften* 98, 397-405. doi: [10.1007/s00114-011-0785-0](https://doi.org/10.1007/s00114-011-0785-0)
- Ravel, A., Marivaux, L., Tabuce, R., Haj Ali, M. B., Essid, E. M., Vianey-Liaud, M., 2012. A new large philisid (Mammalia, Chiroptera, Vespertilionoidea) from the late Early Eocene of Chambi, Tunisia. *Palaeontology* 55, 1035-1041. doi: [10.1111/j.1475-4983.2012.01160.x](https://doi.org/10.1111/j.1475-4983.2012.01160.x)
- Ravel, A., Marivaux, L., Qi, T., Wang, Y. O. Beard, K. C., 2014. New chiropterans from the middle Eocene of Shanghuang (Jiangsu Province, Coastal China): new insight into the dawn horseshoe bats (Rhinolophidae) in Asia. *Zoologica Scripta* 43, 1-23. doi: [10.1111/zsc.12027](https://doi.org/10.1111/zsc.12027)
- Ravel, A., Adaci, M., Bensalah, M., Mahboubi, M., Mebrouk, F., Essid, E. M., Marzougui, W., Khayati Ammar, H., Charruault, A.-L., Lebrun, R., Tabuce, R., Vianey-Liaud, M., Marivaux, L., 2015. New philisids (Mammalia, Chiroptera) from the early-middle Eocene of Algeria and Tunisia: new insight into the phylogeny, palaeobiogeography and palaeoecology of the Philisidae. *Journal of Systematic Palaeontology* 13, 691-709. doi: [10.1080/14772019.2014.941422](https://doi.org/10.1080/14772019.2014.941422)
- Revilliod, P., 1920. Contribution à l'étude des chiroptères des terrains tertiaires. 2. Mémoires de la Société paléontologique Suisse 44, 63-129.
- Roehrs, Z. P., Lack, J. B., Van Den Bussche, R. A., 2010. Tribal phylogenetic relationships within Vespertilioninae (Chiroptera: Vespertilionidae) based on mitochondrial and nuclear sequence data. *Journal of Mammalogy* 91, 1073-1092. doi: [10.1644/09-MAMM-A-325.1](https://doi.org/10.1644/09-MAMM-A-325.1)
- Rose, K. D., Holbrook, L. T., Rana, R. S., Kumar, K., Jones, K. E., Ahrens, H. E., Missiaen, P., Sahni, A., Smith, T., 2014. Early Eocene fossils suggest that the mammalian order Perissodactyla originated in India. *Nature Communications* 5: 5570. doi: [10.1038/ncomms6570](https://doi.org/10.1038/ncomms6570)
- Russell, D. E., Sigé, B., 1970. Révision des chiroptères lutétiens de Messel (Hesse, Allemagne). *Palaeovertebrata* 3, 83-182.
- Russell, D. E., Galoyer, A., Louis, P., Gingerich, P. D., 1988. Nouveaux vertébrés sparnaciens du Conglomérat de Meudon à Meudon, France. *Comptes Rendus de l'Académie des Sciences Paris séries II* 307, 429-433.
- Scotese, C. R., 2006. PALEOMAP Project (<http://www.scotese.com>).
- Sigé, B., 1974. Données nouvelles sur le genre *Stehlinia* (Vespertilionoidea, Chiroptera) du Paléogène d'Europe. *Palaeovertebrata* 6, 253-272.
- Sigé, B., 1985. Les chiroptères Oligocènes du Fayum, Egypte. *Geologica et Palaeontologica*, 19, 161-89.
- Sigé, B., 1991. Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocène inférieur de Tunisie). Aspects biostratigraphique, biogéographique et paléoécologique de l'origine des chiroptères modernes. *Neues Jahrbuch für Geologie und Paläontologie* 182, 355-376.
- Sigé, B., 1995. Le Garouillas et les sites contemporains (Oligocène, MP 25) des phosphorites du Quercy, Lot, Tarn & Garonne, France, et leurs faunes des vertébrés. 5 : Chiroptères. *Palaeontographica A* 236, 77-124.
- Sigé, B., 1997. Les remplissages karstiques polyphasés (Eocène,

- Oligocène, Pliocène) de Saint-Maximin (phosphorite du Gard) et leur apport à la connaissance des faunes européennes, notamment pour l'Eocène moyen (MP 13). 3-Systématique: euthériens entomophages. In: Aguilar, J.-P., Legendre, R.-S., Michaux, J. (Eds.), Actes du Congrès Biochrom'97. Mémoires et Travaux de l'École pratique des Hautes Etudes, Institut de Montpellier, Montpellier, pp. 737-750.
- Sigé, B., Maitre, E., Hand, S. J., 2012. Necromantodonty: the primitive condition of molar morphology in bats. In: Gunnell, G. F., Simmons, N. B. (Eds.) *Evolutionary History of Bats: Fossils, Molecules and Morphology*. Cambridge University Press, Boston, pp. 456-469.
- Simmons, N. B., 2005a. Order Chiroptera. In: Wilson, D. E., Reeder, D. M. (Eds.) *Mammal Species of the World: A Taxonomic and Geographic Reference*, 3rd ed. Smithsonian Institution Press, Washington DC, pp. 312-529.
- Simmons, N. B., 2005b. An Eocene big bang for bats. *Science* 307, 527-528.
- Simmons, N. B., Geisler, J. H., 1998. Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. *Bulletin of the American Museum of Natural History* 235, 1-182.
- Simmons, N. B., Seymour, K. L., Habersetzer, J., Gunnell, G. F., 2008. Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. *Nature* 451, 818-822.
- Slaughter, B. H., 1970. Evolutionary trends of chiropteran dentitions. In: Slaughter, B. H., Walton, D. W. (Eds.), *About Bats*. Southern Methodist University Press, Dallas, pp. 51-83.
- Smith, F. A., Lyons, S. K., Morgan, E. K., Jones, K. E., Kaufman, D. M., Dayan, T., Marquet, P. A., Brown, J. H., Haskell, J. P., 2004. Body mass of Late Quaternary mammals. *Ecological Archives* E084-094. *Ecology* 84, 3403.
- Smith, T., Rana, R. S., Missiaen, P., Rose, K. D., Sahni, A., Singh, H., Singh, L., 2007. High bat (Chiroptera) diversity in the early Eocene of India. *Naturwissenschaften* 94, 1003-1009.
- Smith, T., Habersetzer, J., Simmons, N. B., Gunnell, G. F., 2012. Systematics and paleobiogeography of early bats. In: Gunnell, G. F., Simmons, N. B. (Eds.) *Evolutionary History of Bats: Fossils, Molecules and Morphology*. Cambridge University Press, Boston, pp. 23-66.
- Smith, T., Solé, F., Missiaen, P., Rana, R. S., Kumar, K., Sahni, A., Rose, K. D., 2015. First Early Eocene tapiroid from India and its implication for the paleobiogeographic origin of perissodactyls. *Palaeovertebrata* 39 (2), e5. doi: 10.18563/pv.39.2.e5
- Stadelmann, B., Lin, L.-K., Kunz, T. H., Ruedi, M., 2007. Molecular phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Molecular Phylogenetics and Evolution* 43, 32-48. doi: 10.1016/j.ympev.2006.06.019
- Staub, E. 1998. High-resolution holostratigraphy of middle Paleocene to early Eocene strata in Belgium and adjacent areas. *Palaeontographica A* 247, 91-156.
- Storch, G., Sigé, B., Habersetzer, J., 2002. *Tachypteron franzeni* n. gen., n. sp., earliest emballonurid bat from the Middle Eocene of Messel (Mammalia, Chiroptera). *Paläontologische Zeitschrift* 76, 189-99.
- Storer, J. E., 1984. Mammals of the Swift Current Creek local fauna (Eocene: Uintan), Saskatchewan. *Natural History Contributions (Saskatchewan Culture and Recreation)* 7, 1-158.
- Sudre, J., Erfurt, J. 1996. Les artiodactyles du gisement Yprésien terminal de Prémontré (Aisne, France) In: Godinot, M., Gingerich, P. D. (Eds.), *Volume Jubilaire D.E. Russell*. *Palaeovertebrata* 25, 391-414.
- Tabuce, R., Antunes, M. T., Sigé, B., 2009. A new primitive bat from the earliest Eocene of Europe. *Journal of Vertebrate Paleontology* 29, 627-630.
- Teeling, E. C., Springer, M. S., Madsen, O., Bates, P., O'Brien, S. J., Murphy, W. J., 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science* 307, 580-584.
- Tejedor, M. F., Czaplewski, N. J., Goin, F. J., Aragon, E., 2005. The oldest record of South American bats. *Journal of Vertebrate Paleontology* 25, 990-993.
- Tong, Y.-S., 1997. Middle Eocene small mammals from Liguangqiao Basin of Henan province and Yuanqu Basin of Shanxi province, Central China. *Palaeontologica Sinica* 18, New Series C, 26, 1-256.
- Veilleux, J. P., Whitaker, J. O., Veilleux, S. L., 2003. Tree-roosting ecology of reproductive female eastern pipistrelles, *Pipistrellus subflavus*, in Indiana. *Journal of Mammalogy* 84, 1068-1075.
- Yu, W., Wu, Y., Yang, G., 2014. Early diversification trend and Asian origin for extant bat lineages. *Journal of Evolutionary Biology* 27, 2204-2218. doi:10.1111/jeb.12477
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686-693.

APPENDIX 1

List of Comparative Material Used in this Study

Institutional abbreviations: AMNH American Museum of Natural History, New York, USA; BMNH The Natural History Museum, London, UK; CB Chambi collection, Office National des Mines, Tunis, Tunisia; CM Carnegie Museum of Natural History, Pittsburgh, USA; FNR Université de Montpellier, Fournes Locality collection, France; GMH Geiseltal Museum, Halle, Germany; GPIMUH Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Germany; GU/RSR/VAS Garhwal University, Srinigar, India; HLMD Hessisches Landesmuseum, Darmstadt, Germany; IITR/SB/VLM Indian Institute of Technology, Roorkee, India; IRSNB M Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; IVPP V Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LIEB-PV Laboratorio de Investigaciones en Evolución y Biodiversidad, Universidad Nacional de la Patagonia —San Juan Bosco, Argentina; MNHN Muséum National d'Histoire Naturelle, Paris, France; QM Queensland Museum, Brisbane, Australia; ROM Royal Ontario Museum, Toronto, Canada; SMF Me Senckenberg Museum, Messel Department, Frankfurt, Germany; SMNK Staatliches Museum für Naturkunde, Karlsruhe, Germany; UM Université de Montpellier, Montpellier, France; UNLSNC Universidade Nova de Lisboa, Portugal, Silveirinha new collection; UT University of Tlemcen, Tlemcen, Algeria; UW University of Wyoming Museum, Laramie, Wyoming, USA; YPM-PU Princeton University (collections now housed in the Yale Peabody Museum, New Haven, CT, USA).

In the list below, *denotes original material examined in addition to (otherwise) primary literature, supplementary photographs and/or scan data for all specimens. Families listed alphabetically.

Archaeonycteridae: *Archaeonycteris trigonodon* Revilliod, 1917 Grube Messel near Darmstadt, Germany HLMD 1398-Me 33a, b*, HLMD 16069; *A. brailioni* Russell *et al.*, 1973, Mutigny and Avenay, Marne, France MNHN Louis-410 Mu, MNHN Louis-432 Mu*, MNHN Bn-751 Av*, MNHN Bn-757 Av* (cast SMF 77/262); *A. pollex* Storch & Habersetzer, 1988 Grube Messel near Darmstadt, Germany SMNK Me 982*; *A. relictia* Harrison & Hooker, 2010 Creechbarrow, Dorset, England BMNH M35710/12; ?*A. praecursor* Tabuce *et al.*, 2009 Silveirinha Portugal UNLSNC-447*; ?*A. storchi* Smith *et al.*, 2007 Vastan lignite mine, Gujarat, India GU/RSR/VAS 140; cf. *Archaeonycteris* sp. (*sensu* Smith *et al.*, 2012; cf. *Icaronycteris* sp. in Russell *et al.*, 1988) Meudon, France MNHN 16065 Me*; *Protonycteris gunnelli* Smith *et al.*, 2007 Vastan lignite mine, Gujarat, India GU/RSR/VAS 436. **Hassianycteridae:** *Hassianycteris revilliodi* (Russell & Sigé, 1970) Grube Messel near Darmstadt, Germany HLMD 4294 Me 16* (cast SMF 77/269). *H. messelensis* Smith & Storch, 1981, Grube Messel near Darmstadt, Germany HLMD Me 7480*; *H. magna*

Smith & Storch, 1981, Grube Messel near Darmstadt, Germany HLMD Me 7539*; *H. kumari* Smith *et al.*, 2007 Vastan lignite mine, Gujarat, India GU/RSR/VAS 56, GU/RSR/VAS 561; *Cambaya complexus* Bajpai *et al.*, 2005 Vastan lignite mine, Gujarat, India IITR/SB/VLM 435. **Icaronycteridae:** *Icaronycteris index* Jepsen, 1966; Green River Formation, Wyoming, USA, YPM-PU 18150* and UW 21481*; *I. menui* Russell *et al.*, 1973 Mutigny and Avenay, Marne, France MNHN Louis-333*, MNHN Louis-Mu*, MNHN Louis-331*, MNHN Louis-380*, MNHN Louis-384*, MNHN Louis-353*, MNHN Louis-357*, MNHN Louis-117*, MNHN Av7201*, MNHN Av6797*, MNHN Av7200*, MNHN Louis-360 Mu*, MNHN Bn-547 Av*, MNHN Bn-340 Av*, MNHN Bn-319 Av* (SMF 77/259-261); *I. sigei* Smith *et al.*, 2007 Vastan lignite mine, Gujarat, India GU/RSR/VAS 137. **Mixopterygidae:** *Carcinopteryx maximinensis* Maitre *et al.*, 2008 from St-Maximin, Gard Phosphorites, France, UM-SMXCm A.1.3*, UM-SMXCm A.1.5*. **Onychonycteridae:** *Onychonycteris finneyi* Simmons *et al.*, 2008 Green River Formation, Wyoming, USA, ROM 55351A,B*, AMNH FM 142467*; *Ageina tobieni* Russell *et al.*, 1973 Mutigny, Marne, France MNHN Mu 5112*, MNHN Louis-481 Mu* (cast SMF 77/263); *Eppsinycteris anglica* (Cooper, 1932) Abbey Wood, London Basin, England BMNH M13776; *Honrovits tsuwape* Beard *et al.*, 1992 Wind River Formation, Wyoming, USA CM62640*, CM 62641*; ?*Honrovits joeli* (Smith & Russell, 1992) Evere, Belgium IRSNB M 1567 (cast); *Marnenycteris michauxi* Hand *et al.*, 2015 Pourcy, France UM POY-11. **Palaeochiropterygidae:** *Palaeochiropteryx tupaiodon* Grube Messel near Darmstadt, Germany HLMD Me25* (cast SMF 77/271 and 272), Me 266* (cast SMF 77/273 and 274); *Palaeochiropteryx spiegelii* Grube Messel near Darmstadt, Germany HLMD Me32 * (cast SMF 77/270); *Cecilonycteris prisca* Heller, 1935 Geiseltal Obere Mittelkohle, Germany, GMH 3965*; *Matthesia germanica* Sigé & Russell, 1980, Geiseltal Obere Mittelkohle, Germany, GMH 3940*; *Lapichiropteryx xiei* Tong, 1997 Tuqiaogou, Shanxi province, China IVPP V10204; *Microchiropteryx folieae* Smith *et al.*, 2007 Vastan lignite mine, Gujarat, India GU/RSR/VAS 459. **Philisidae:** *Dizya exsultans* Sigé, 1991 Chambi, Tunisia CB 1-15*; *Witwatia schlosseri* Gunnell *et al.*, 2008 Fayum, Egypt; *Philisis sphingis* Sigé, 1985 Fayum, Egypt. **Family incertae sedis:** *Australonycteris clarkae* Hand *et al.*, 1994 Murgon, Queensland, Australia QM F19147, QM F19149*; *Jaegeria cambayensis* Bajpai *et al.*, 2005 Vastan lignite mine, Gujarat, India IITR/SB/VLM/585; Chiropteran (Tejedor *et al.*, 2005) Laguna Fría, Chubut Province, Argentina, LIEB-PV 999; Chiroptera indet. 2 (Marandat, 1991) Fournes, Minervois, France FNR-02*; Eochiroptera (Ravel *et al.* 2011) El Kohol, Algeria UT-KD-02, UT-KD-03.