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ORIGINAL PAPER

Global Completeness of the Bat Fossil Record

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Abstract Bats are unique among mammals in their use of powered flight and their widespread capacity for laryngeal echolocation. Understanding how and when these and other abilities evolved could be improved by examining the bat fossil record. However, the fossil record of bats is commonly believed to be very poor. Quantitative analyses of this record have rarely been attempted, so it has been difficult to gauge just how depauperate the bat fossil record really is. A crucial step in analyzing the quality of the fossil record is to be able to accurately estimate completeness. Measures of completeness of the fossil record have important consequences for our understanding of evolutionary rates and patterns among bats. In this study, we applied previously developed statistical methods of analyzing completeness to the bat fossil record. The main utility of these methods over others used to study completeness is their independence from phylogeny. This phylogenetic-independence is desirable, given the recent state of flux in the higher-level phylogenetic relationships of bats. All known fossil bat genera were tabulated at the geologic stage or sub-epoch level. This binning strategy allowed an estimate of the extinction rate for each bat genus per bin. Extinction rate—together with per-genus estimates of preservation probability and original temporal distributions—was used to calculate completeness. At the genus level, the bat fossil record is estimated to be 12% complete. Within the order, Pteropodidae is missing most of its fossil history, while Rhinolophoidea and Vespertilionoidea are missing the least. These results suggest that 88% of bats that existed never left a fossil record, and that the fossil record of bats is indeed poor. Much of the taxonomic and evolutionary history of bats has yet to be uncovered.

Keywords Chiroptera · Completeness · Fossil record · Phylogeny-independent

Introduction

Fossils provide the only direct evidence concerning the diversity of life through time, and as such they are paramount in studies of evolutionary patterns and rates. Macroevolutionary studies that address such issues typically employ the relatively densely sampled invertebrate fossil record (e.g., Foote and Raup 1996; Cheetham and Jackson 1998). However,

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several vertebrate groups have well-sampled fossil records whose long-term evolutionary histories have been thoroughly studied by paleobiologists. Among fossil mammals, most work that pertains to macroevolutionary patterns and processes involves either large-scale analyses of terrestrial land-mammals through the Cenozoic (e.g., Foote and Raup 1996; Alroy 2000), detailed examinations of relatively short, densely sampled fossil occurrences (e.g., Clyde and Gingerich 1994; Alba et al. 2001; Wood et al. 2007), or, less commonly, investigations at scales intermediate between these two (e.g., MacFadden 1985). In most cases, these studies have been restricted to taxonomic groups that have been studied extensively and for which considerable diversity or abundance of fossil forms is thought to be present. Evolutionary patterns in the fossil record of relatively poorly sampled groups have been only rarely examined.

One conspicuous group for which macroevolutionary analyses using the fossil record have been rare is bats (Mammalia: Chiroptera). With more than 1100 extant species (Simmons 2005), bats comprise an extraordinary taxonomic diversity that is second only to rodents among living mammals. Phylogenetic investigations of bats have provided some important insights into the evolutionary history of the group, including recent efforts reaffirming bat monophyly and uncovering various hypotheses of microchiropteran paraphyly. In principal, a perfect fossil record would illuminate the correct phylogenetic history of bats; such a record might serve as an independent test of the correctness of various phylogenetic hypotheses. However, few studies of bats have incorporated extinct taxa into phylogenetic analyses, especially in genus- or species-level analyses. Using fossils in systematics will likely become less common as molecular-based systematics continues to proliferate (Hermsen and Hendricks 2008). However, depending on the types of hypotheses being tested, ignoring fossil taxa that contain phylogeny-relevant information not found in extant organisms may limit our potential to completely understand the evolutionary histories of these groups and may even produce misleading results in some instances.

To determine the potential utility of the bat fossil record in illuminating patterns of evolution, an understanding of its quality must be assessed. How accurately does the known fossil record reflect the true evolutionary history of bats? Two conceptual approaches have been used to address this question in other groups of animals. The first is phylogeny-dependent, in which the quality of the fossil record is assessed for a particular phylogeny. Teeling et al. (2005) presented one type of phylogeny-dependent method of assessing the fossil record of bats. They generated Bayesian estimates of divergence dates for each of the 58 branches (internal and terminal) from their maximum likelihood tree. Teeling et al. then compared their molecular divergence estimates with the oldest known fossils from the 58 branches of the tree. They used the differences in ages between the molecular and fossil estimates to calculate a percentage of missing fossil data per branch. The results of their analyses estimated that, on average, 73% of the known fossil record of 58 lineages of bats was missing. Pteropodid bats, long known to have a poorly sampled record, were missing upwards of 98% of their fossil history. The four non-pteropodid superfamilies were missing between 56% and 86% of their fossil record. Thus, the results of the Teeling et al. (2005) study seem to show that the fossil record of bats is quite poor. However, methods like that presented in Teeling et al. (2005) are heavily dependent upon the lineages included and the topology of the phylogeny used. Due to recent volatility in hypotheses of the higher-level phylogenetic relationships of bats (Springer et al. 2001; Jones et al. 2002, 2005; Eick et al. 2005; Gunnell and Simmons 2005; Teeling et al. 2005; Hermsen and Hendricks 2008), there may be some uncertainty in estimating the quality of the fossil record of bats using phylogeny-dependent methods.

Fortunately, the second class of methods for assessing the quality of the fossil record is phylogeny-independent. That is, statistical metrics are applied directly to the fossil data that quantify the quality of the fossil record (Benton 1998; Paul 1998). The method developed by Foote and Raup (1996) allows for one such quantitative analysis of the fossil record for any group independent of phylogeny. By estimating preservation probability, extinction rate, and the stratigraphic duration of taxa, *completeness* can be calculated deterministically. Completeness is defined as “the proportion of taxa that have left some fossil record,” (Foote and Raup 1996; *sensu* Valentine 1989), and it therefore serves as a metric for assessing the quality of the fossil record. In this paper we address the quality of the bat fossil record by calculating completeness using the method presented in Foote and Raup (1996). We calculate completeness for Chiroptera as a whole, as well as for the major higher-level bat clades. These calculations allow for a comparison of the fossil record for each of these groups, as well as an assessment of the quality of the fossil record of bats using a method independent of phylogeny.

Materials and methods

Data collection

A database of all known fossil bat genera was compiled from the literature Appendix (1). Genera were tabulated according to their temporal and geographic distribution. Taxonomy followed Simmons (2005), with the exceptions of *Perimyotis* and *Parastrellus*, which were considered distinct genera following the recommendations of Hoofer et al. (2006). Miniopteridae was considered to be a distinct family, following recommendations of recent analyses (e.g., Miller-Butterworth et al. 2007). Superfamily membership followed Teeling et al. (2005). Specimens identified as “cf.” (e.g., “cf. *Eptesicus* indet.”) were considered valid records for recording presence/absence. Pre-Pleistocene fossil bats were assigned to one of fifteen chronostratigraphic stages: Ypresian, Lutetian, Bartonian, Priabonian, Rupelian, Chattian, Aquitanian, Burdigalian, Langhian, Serravalian, Tortonian, Messinian, Zanclean, Piacenzian, and Gelasian. The Pleistocene was tabulated as a single bin. Stages and boundary dates were taken from Gradstein et al. (2004). Correlation of the European Mammal Neogene (MN) system was performed using Agustí et al. (2001) and references therein. Recent genera were tabulated and used for comparative purposes (but not for statistical calculations).

Data analysis

Calculations of completeness were carried out according to the discrete-time and infinite-window method of Foote and Raup (1996). This method requires tabulating the ranges of all taxa (bat genera in this case) according to discrete time intervals (mostly stages or combinations of two to three stages for this study). Our binning strategy attempted to produce bins of roughly equal durations. Thus, we summed several smaller bins into fewer large bins in an effort to combat high variance in the duration of stages in the Cenozoic (older stages tend to be longer than younger). In particular, we grouped all of the middle Miocene, all of the late Miocene, and all of the Plio-Pleistocene together into three bins (instead of the eight stages that fall within these time periods). The range of a taxon preserved in only one time interval is one. Stratigraphic data are tabulated using first and last occurrences, so that the range of a taxon equals the number of time intervals between its first and last occurrences, including the endpoints. Preservation probability *R* (the probability that a taxon is preserved at least once in an interval) was estimated by using the frequency, *f*, of taxa with observed ranges of one, two, and three intervals to calculate the range-frequency ratio, *FreqRat*, as:

$$R \approx FreqRat = f(2)^2 \Big/ [f(1)f(3)]$$

Estimated preservation probability must be considered with respect to true durations, so calculating *R* is insufficient to analyze the quality of the fossil record (Foote and Raup 1996; Alba et al. 2001). Therefore, the probability $P_1(T)$ that a taxon is preserved at least once given a true original duration *T* must be calculated:

$$P_1(T) = 1 - (1 - R)^T$$

Original durations can be calculated assuming a constant extinction rate *q* (and exponential distribution of original durations), where *q* is calculated from the ln-slope of range-frequencies (omitting taxa that occur in only one bin) as the slope with the sign reversed (see Fig. 1). The probability *h(T)* that the original distribution equals *T* is calculated as:

$$h(T) = e^{-q(T-1)} - e^{-qT}$$

Completeness P_p is calculated as the sum, for all original durations (i.e., T=1-∞), of the product between *h(T)* (probability of having original duration *T*) and $P_1(T)$ (probability of being preserved at least

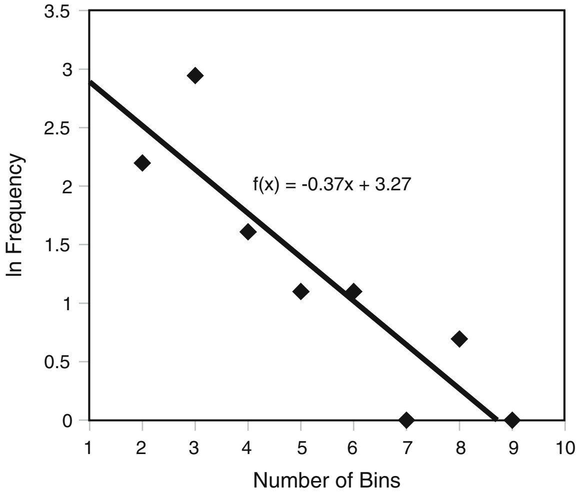

Fig. 1 Natural-log plot of range frequencies for fossil bat genera. Regression line was calculated after excluding genera with frequencies of zero or one bin. The slope of the regression line with the sign reversed equals extinction rate ($q = 0.37$).

once during an interval given an original duration T) as:

$$P_p = \sum_{T=1}^{\infty} h(T) P_1(T)$$

P_p was calculated for the pooled data, such that the range of each genus was considered only on a worldwide basis. Thus, P_p was considered an estimate of global completeness. To explore the differences among the bat fossil record of various clades within Chiroptera, P_p was calculated separately for Pteropodidae, Rhinolophoidea, Emballonuroidea, Noctilionoidea, and Vespertilionoidea (*sensu* Teeling et al. 2005), with varying degrees of success. A worked example of the statistical calculations, using the vespertilionoid data, is provided in Appendix 2.

Results

Preservation probability, extinction rate (Fig. 1), and completeness are presented in Table 1 for all calculations. No calculations were possible for Pteropodidae, Emballonuroidea, or Noctilionoidea. Approximately half of all genera in the database were represented at least once in the fossil record (143/277). Of all extant genera, approximately 35% (71/204) are known as fossils. There are 70 known extinct bat genera. Approximately 72% of the genera had a range of one stratigraphic horizon. Those genera lasting two stages comprised about 6% of the genera, while those lasting three stages accounted for 13% of the data. Every other range-duration contained fewer than 5% of the genera.

The number of known genera through time for six clades (Chiroptera, Pteropodidae, and the four superfamilies Rhinolophoidea, Emballonuroidea, Noctilionoidea, and Vespertilionoidea) plus a group of genera from all extinct and uncertain families is shown in Fig. 2. For Chiroptera as a whole, generic diversity is currently at its peak, with a relatively high diversity extending back through the Pleistocene. There has been an apparent gradual increase in diversity through time. Fossil Pteropodidae are rare at the genus level, with only three Tertiary occurrences. Rhinolophoidea (Hipposideridae, Megadermatidae, Craseonycteridae, Rhinopomatidae, and Rhinolophidae), the clade that newer studies suggest may share a sister relationship with pteropodid bats

Table 1 Calculations of preservation probability, extinction rate, and completeness for all bats (Chiroptera) and the two superfamilies Rhinolophoidea and Vespertilionoidea

Analysis	Number of taxa (n)[1]	Preservation probability (R)	Extinction rate (q)	Correlation coeff. (r) of q	Completeness (P_p)	P_p analog from Teeling et al. (2005)
Chiroptera	143	0.04	0.37	0.9	0.12	0.27
Rhinolophoidea	21	0.03	0.1	0.51	0.25	0.44
Vespertilionoidea	56	0.08	0.32	0.76	0.25	0.40

[1] fossil genera only

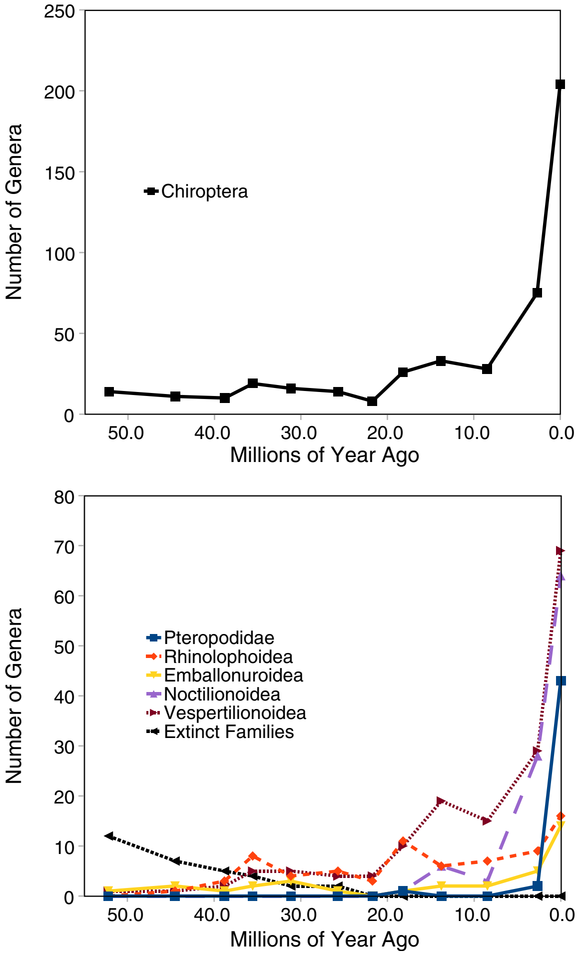

Fig. 2 Number of fossil bat genera through time. All Recent bat genera are plotted for comparison with fossil forms. Each point corresponds to the middle of the bin it represents (except for the Recent). For both graphs, the *x*-axis plots time in millions of years ago, and the *y*-axis plots the number of genera. Note the different scales of the *y*-axis between the top and bottom graphs.

(e.g., Jones et al. 2005; Teeling et al. 2005), shows relatively high generic diversity (compared to modern) throughout most of its history, after initially low diversity during the middle Eocene. Diversity in several intervals throughout the Tertiary (e.g., Rupelian, Burdigalian) approaches or surpasses that of the Pleistocene; only Recent rhinolophoid diversity is higher. Emballonuroidea (Emballonuridae and Nycteridae) are present in relatively low generic diversity throughout the Tertiary, with a slight increase in the Pleistocene and a peak in diversity during the Recent. Noctilionoidea (Furipteridae, Miniopteridae, Mormoopidae, Mystacinidae, Myzopodidae, Noctilionidae, Phyllostomidae, and Thyropteridae) are unknown at the genus level until the Burdigalian (late early Miocene), and they maintain a very low diversity throughout the remainder of the Tertiary. Many more genera are known from the Pleistocene, and the Recent contains the highest noctilionoid diversity. Vespertilionoidea, similar to the patterns in other groups, shows a peak in diversity during the Recent. Generic diversity in vespertilionoids is relatively high throughout much of the Neogene; from 10 to 20 genera are known from each stage of the Neogene after the Aquitanian (early Miocene).

Discussion

The global completeness estimate of 12% indicates that the bat fossil record is very poor. In other words, approximately 88% of all bats that lived never left a fossil record. This low completeness figure lends credence to the notion that bats have a poor fossil record, and it suggests that much of the evolutionary history of the group cannot be studied using fossil data. Teeling et al. (2005) found similar results—the origins of 73% of the 58 bat lineages in their analyses were underestimated by the fossil record. Importantly, their results were calculated using phylogeny-dependent methods, so general congruence between their figure and ours probably reflects a real phenomenon; namely, bats have a poor fossil record.

Calculations from other taxonomic groups, though not directly comparable, typically provide much higher completeness estimates (e.g., P_p=0.58 for extinct, North American Cenozoic non-volant mammal species [Foote and Raup 1996], and P_p=0.91 for mammals from the Neogene of Spain and Portugal [Alba et al. 2001]). Such a low completeness value for bat genera relative to these other studies may in part be due to the global nature of this study; local completeness for a restricted stratigraphic section typically results in much higher values (e.g., Cheetham and Jackson 1998). Such studies are usually performed when fossils are sampled densely in regions with few lapses in the rock record (Foote and Raup 1996). Furthermore, choice of taxa may play a role, and bats are probably less easily preserved than other mammals for both anatomical (delicate skeletons) and taphonomic reasons (see discussion below). This effect may be partly responsible for the high proportion of single hits in the data set (72% of all fossil bats occur in just one bin). Foote and Raup (1996) warn that high proportions of single hits may produce very high variances in estimates of original durations, which produce large errors when calculating completeness.

Fossil bats presumably inhabited environments similar to their modern counterparts, which typically are not well sampled in the fossil record. Of the common bat habitats, caves offer some of the best conditions for preservation, and many fossil bats are known from cave and karst deposits (Kowalski 1995). For example, Tertiary bats from the Mediterranean basin typically come from karst deposits (Sigé and Legendre 1983) and many bats from the Miocene Riversleigh Site of Australia apparently come from cave-fill deposits as well (Hand and Archer 2005). Other than caves, many of the best preserved fossil bats come from sedimentary deposits of extinct lakes (e.g., Jepsen 1966; Habersetzer and Storch 1987; Gunnell et al. 2003; Simmons et al. 2008); lacustrine environments provide some of the best conditions for fossilization in the terrestrial realm. Unfortunately, most bats visit lakes only briefly, so their potential for fossilization in these environments usually is very low.

A rather striking result is the general match between the superfamily-level results from Teeling et al. (2005) with those from this study (Fig. 2), though Teeling et al. found consistently higher completeness figures for each clade (Table 1). The rank-order from most to least percent missing from Teeling et al. (2005) is: Pteropodidae, Noctilionoidea, Emballonuroidea, Rhinolophoidea, and Vespertilionoidea. In the present study, completeness was calculated for Rhinolophoidea and Vespertilionoidea (in addition to all Chiroptera). Calculations were not possible for Pteropodidae, Noctilionoidea, or Emballonuroidea because of too little data. As Table 1 shows, the calculations of extinction rate (q) yielded Pearson coefficients of correlation (between the number of stages and the natural log of the frequency of genus occurrences) of 0.51 for Rhinolophoidea and 0.76 for Vespertilionoidea. The higher correlation for Vespertilionoidea may mean that the extinction rate is more reliable as compared to Rhinolophoidea. Furthermore, because the extinction rate is used to calculate completeness, the completeness of Vespertilionoidea may be more robust than it is for Rhinolophoidea.

It is important to note that having too little data to calculate completeness for Pteropodidae, Noctilionoidea, and Emballonuroidea does not, by itself, mean that the fossil records for these three groups are woefully incomplete. Our binning strategy may have been too aggressive in lumping together into the same bin bats that were found in different stratigraphic levels. If these three clades were geologically rather young (middle or late Miocene, for example), then there would not be enough binned intervals to generate a sufficient statistical sample to calculate completeness. However, none of these three clades are young, as shown by their fossil ages (Appendix 1, Fig. 2) and by phylogenetic analyses (Teeling et al. 2005; Gunnell and Simmons 2005). Examining the pattern of fossil occurrences through time (Fig. 2) provides some insight into the quality of the record for each of these groups. When compared to their modern diversity, Pteropodidae and Noctilionoidea seem to have the worst records, while Rhinolophoidea and Vespertilionoidea have the best. If we compare groups of similar modern generic diversity, it seems that Vespertilionoidea has a better record than Noctilionoidea, as does Rhinolophoidea when compared to Emballonuroidea. Completeness values for Rhinolophoidea and Vespertilionoidea were twice that of Chiroptera as a whole (25% versus 12%). So, it is reasonable to expect that groups other than the rhinolophoids and vespertilionoids would have completeness values substantially lower than 12% (though parsing out completeness values for each of these other groups was not possible in the present study).

Considering the apparent dual sister-group relationships between Noctilionoidea and Vespertilionoidea on the one hand, and Rhinolophoidea and Pteropodidae on the other (e.g., Jones et al. 2005), the apparent disparity in the quality of their fossil records cannot be attributed to factors affecting all bats. In part, the time available for diversification may have differentially affected clades, considering that the generic-rich noctilionoid family Phyllostomidae may be much younger than either Molossidae or Vespertilionidae that together comprise most of the vespertilionoid diversity. But even in the Miocene—likely after the origin of the first phyllostomid (Jones et al. 2005)—the vespertilionoid record contains much more diversity than the noctilionoid record. So, the disparity in the fossil records may in part be a real phenomenon that can be explained by at least three non-exclusive factors. First, it probably reflects a collector bias, as vespertilionoids and rhinolophoids constitute a disproportionate share of the bat fossils known from Europe and North America, both of which have a rather good sampling of fossil forms (Gunnell and Simmons 2005; Hulva et al. 2007). An increased sampling effort throughout the Old and New World tropics may diminish the problem of a depauperate bat fossil record, at least to some degree. Second, differences in the quality of the fossil record between bat clades could be due to different taphonomic effects. Pteropodids and most noctilionoids today inhabit tropical regions in which environmental conditions offer little hope of becoming fossils. For temperate bats, dominated by vespertilionoids, a large percentage inhabits caves and faces fewer taphonomic impediments to fossilization immediately after death. Finally, the disparity in the fossil record of bat clades could be due to a poor rock record. In this case, it may be that diverse assemblages of poorly represented bat clades were fossilized, but these fossils have been buried or destroyed as a result of subsequent geologic processes. Different bat clades could have experienced high diversity at different points in time, and some of these time periods may have been preferentially lost in the rock record.

While numerous questions cannot be directly addressed with this study (e.g., paleobiogeographic patterns), the results confirm the notion that the genus-level fossil record of bats is poor. As such, it is unclear how incorporating extinct bat genera into phylogenetic analyses would really enhance the resulting phylogenetic hypotheses, though simulations indicate that, even in the face of very high degrees of incompleteness, incorporating fossil data can improve phylogeny estimation (Fox et al. 1999). Some studies have shown a fairly high degree of consistency between phylogenetic analyses that do and do not incorporate extinct forms and their stratigraphic positions (e.g., Norell and Novacek 1992); others have demonstrated that fossils play a critical role in phylogeny estimation (e.g., Gauthier et al. 1988). Unfortunately, fossil bats often are represented by little more than isolated teeth or, at best, mandibular or maxillary fragments (Czaplewski et al. 2008). Though numerous parsimony-informative characters are found in the skull and dentition, many diagnostic characters are found in other parts of the skeleton (e.g., Gunnell et al. 2003; Simmons et al. 2008), and an absence of sufficient material may preclude definitive taxonomic or character assignment. Many important early bats cannot be assigned to genera (or even higher level groups) with any certainty (e.g., Archer 1978; Ducrocq et al. 1993; Tejedor et al. 2005). Such specimens have been omitted from this study, as we await more diagnostic material. However, any estimate of the completeness of the fossil record is predicated on the assumption that taxonomic diagnoses have been made correctly, so this issue may not preferentially bias our results.

Conclusions

This study marks the first phylogeny-independent estimate of the global completeness of the fossil record of bats. The genus-level bat fossil record is estimated to be 12% complete. This figure agrees broadly with phylogeny-derived completeness estimates by Teeling et al. (2005) in confirming the notion that the bat fossil record is poor. Such results indicate that much of the taxonomic and morphologic diversity of bats remains to be uncovered. Despite the depauperate fossil record, important steps in the evolutionary history of bats are recorded in fossils, such as the apparent evolution of flight before high-frequency echolocation in Eocene bats (Simmons et al. 2008). Future work should examine Tertiary deposits from historically under-sampled regions to increase our knowledge of fossil bats and thus improve our understanding of this remarkable group of mammals.

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Appendix 1

Table 2 Compilation of bat fossil genera used in this study. Temporal records of bat genera were tabulated as present (1) or absent (0) in each discrete time interval. Sources, shown below the table, record the first and last occurrences of each genus (excluding Recent), plus additional intervening occurrences when available (non-exhaustive). Secondary sources were used in cases where primary sources were unavailable. Stratigraphic bin abbreviations as follows: Eo = Eocene, Oligo = Oligocene, Mio = Miocene, P-P = Pliocene through Pleistocene, Rec = Recent; Ypr = Ypresian, Lut = Lutetian, Bart = Bartonian, Pria = Priabonian, Rup = Rupelian, Chat = Chattian, Aqui = Aquitanian, Burd = Burdigalian, M Mio = Middle Miocene, L Mio = Late Miocene. Ma = Millions of Years Ago. Records for Recent bats were not used in statistical calculations

Superfamily	Family	Genus	Eo				Oligo		Mio				P-P	Rec	Source
		Ma:	Ypr 55.8	Lut 48.6	Bart 40.4	Pria 37.2	Rup 33.9	Chat 28.4	Aqui 23.0	Burd 20.4	M Mio 16.0	L Mio 11.6	P-P 5.3	Rec 0.012	
Emballonuroidea	?Emballonuridae	*†Eppsinycteris*	1	0	0	0	0	0	0	0	0	0	0	0	63
Emballonuroidea	Emballonuridae	*†Dhofarella*	0	0	0	1	1	0	0	0	0	0	0	0	44, 118
Emballonuroidea	Emballonuridae	*†Tachypteron*	0	1	0	0	0	0	0	0	0	0	0	0	127
Emballonuroidea	Emballonuridae	*†Vespertiliavus*	0	1	1	1	1	1	0	0	0	0	0	0	6, 35, 82, 114, 139
Emballonuroidea	Emballonuridae	*Balantiopteryx*	0	0	0	0	0	0	0	0	0	0	1	1	34
Emballonuroidea	Emballonuridae	*Centronycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Emballonuroidea	Emballonuridae	*Coleura*	0	0	0	0	0	0	0	0	0	0	1	1	141
Emballonuroidea	Emballonuridae	*Cormura*	0	0	0	0	0	0	0	0	0	0	0	1	
Emballonuroidea	Emballonuridae	*Cyttarops*	0	0	0	0	0	0	0	0	0	0	0	1	
Emballonuroidea	Emballonuridae	*Diclidurus*	0	0	0	0	0	0	0	0	1	1	1	1	18
Emballonuroidea	Emballonuridae	*Emballonura*	0	0	0	0	0	0	0	0	0	0	0	1	
Emballonuroidea	Emballonuridae	*Mosia*	0	0	0	0	0	0	0	0	0	0	0	1	
Emballonuroidea	Emballonuridae	*Peropteryx*	0	0	0	0	0	0	0	0	0	0	1	1	24
Emballonuroidea	Emballonuridae	*Rhynchonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Emballonuroidea	Emballonuridae	*Saccolaimus*	0	0	0	0	0	0	0	0	0	0	1	1	13, 141
Emballonuroidea	Emballonuridae	*Saccopteryx*	0	0	0	0	0	0	0	0	0	0	0	1	
Emballonuroidea	Emballonuridae	*Taphozous*	0	0	0	0	0	0	0	1	1	1	1	1	11, 76
Emballonuroidea	Nycteridae	*†Chibanycteris*	0	0	0	0	1	0	0	0	0	0	0	0	118
Emballonuroidea	Nycteridae	*Nycteris*	0	0	0	0	0	0	0	0	0	0	1	1	9, 92
Extinct	?Hassianycteridae	*†Cambaya*	1	0	0	0	0	0	0	0	0	0	0	0	124
Extinct	†Archaeonycteridae	*†Archaeonycteris*	1	1	1	0	0	0	0	0	0	0	0	0	97, 103, 120, 124
Extinct	†Archaeonycteridae	*†Protonycteris*	1	0	0	0	0	0	0	0	0	0	0	0	124

Extinct	†Hassianycteridae	*†Hassianycteris*	1	1	0	0	0	0	0	0	0	0	0	0	122, 123
Extinct	†Icaronycteridae	*†Icaronycteris*	1	0	0	0	0	0	0	0	0	0	0	0	68, 97, 103
Extinct	†Incertae cedis	*†Ageina*	1	0	0	0	0	0	0	0	0	0	0	0	103
Extinct	†Incertae cedis	*†Alastorius*	0	0	0	0	0	1	0	0	0	0	0	0	42, 129
Extinct	†Incertae cedis	*†Archaeopteropus*	0	0	0	0	1	0	0	0	0	0	0	0	42, 83
Extinct	†Incertae cedis	*†Australonycteris*	1	0	0	0	0	0	0	0	0	0	0	0	57
Extinct	†Incertae cedis	*†Chadronycteris*	0	0	0	1	0	0	0	0	0	0	0	0	91
Extinct	†Incertae cedis	*†Jaegeria*	1	0	0	0	0	0	0	0	0	0	0	0	124
Extinct	†Mixopterygidae	*†Carcinipteryx*	0	1	1	1	0	0	0	0	0	0	0	0	81
Extinct	†Mixopterygidae	*†Mixopteryx*	0	0	0	1	1	1	0	0	0	0	0	0	81
Extinct	†Onychonycteridae	*†Onychonycteris*	1	0	0	0	0	0	0	0	0	0	0	0	121
Extinct	†Palaeochiropterygidae	*†Cecilionycteris*	0	1	0	0	0	0	0	0	0	0	0	0	59
Extinct	†Palaeochiropterygidae	*†Lapichiropteryx*	0	0	1	0	0	0	0	0	0	0	0	0	133
Extinct	†Palaeochiropterygidae	*†Matthesia*	0	1	0	0	0	0	0	0	0	0	0	0	116
Extinct	†Palaeochiropterygidae	*†Microchiropteryx*	1	0	0	0	0	0	0	0	0	0	0	0	124
Extinct	†Palaeochiropterygidae	*†Palaeochiropteryx*	1	1	1	0	0	0	0	0	0	0	0	0	99, 106
Extinct	†Tanzanycteridae	*†Tanzanycteris*	0	1	0	0	0	0	0	0	0	0	0	0	43
Noctilionoidea	Furipteridae	*Amorphochilus*	0	0	0	0	0	0	0	0	0	0	1	1	86
Noctilionoidea	Furipteridae	*Furipterus*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Mormoopidae	*Mormoops*	0	0	0	0	0	0	0	0	0	0	1	1	87, 119
Noctilionoidea	Mormoopidae	*Pteronotus*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Mystacinidae	*†Icarops*	0	0	0	0	0	0	0	1	1	0	0	0	56
Noctilionoidea	Mystacinidae	*Mystacina*	0	0	0	0	0	0	0	0	0	0	1	1	10, 146
Noctilionoidea	Myzopodidae	*Myzopoda*	0	0	0	0	0	0	0	0	0	0	1	1	10
Noctilionoidea	Noctilionidae	*Noctilio*	0	0	0	0	0	0	0	0	1	1	1	1	18, 22, 31
Noctilionoidea	Phyllostomidae	*†Notonycteris*	0	0	0	0	0	0	0	0	1	0	0	0	31, 105
Noctilionoidea	Phyllostomidae	*†Palynephyllum*	0	0	0	0	0	0	0	0	1	0	0	0	31
Noctilionoidea	Phyllostomidae	*Ametrida*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Anoura*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Ardops*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Ariteus*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Artibeus*	0	0	0	0	0	0	0	0	0	0	1	1	24, 34
Noctilionoidea	Phyllostomidae	*Brachyphylla*	0	0	0	0	0	0	0	0	0	0	1	1	84, 119
Noctilionoidea	Phyllostomidae	*Carollia*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Phyllostomidae	*Centurio*	0	0	0	0	0	0	0	0	0	0	0	1	

Table 2 (continued)

Superfamily	Family	Genus	Eo				Oligo		Mio				P-P	Rec	Source
			Ypr	Lut	Bart	Pria	Rup	Chat	Aqui	Burd	M Mio	L Mio	P-P	Rec	
		Ma:	55.8	48.6	40.4	37.2	33.9	28.4	23.0	20.4	16.0	11.6	5.3	0.012	
Noctilionoidea	Phyllostomidae	*Chiroderma*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Phyllostomidae	*Choeroniscus*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Choeronycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Chrotopterus*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Phyllostomidae	*Desmodus*	0	0	0	0	0	0	0	0	0	0	1	1	24, 26, 89
Noctilionoidea	Phyllostomidae	*Diaemus*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Diphylla*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Phyllostomidae	*Ectophylla*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Enchisthenes*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Erophylla*	0	0	0	0	0	0	0	0	0	0	1	1	87, 119
Noctilionoidea	Phyllostomidae	*Glossophaga*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Glyphonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Hylonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Lampronycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Leptonycteris*	0	0	0	0	0	0	0	0	0	0	1	1	34
Noctilionoidea	Phyllostomidae	*Lichonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Lionycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Lonchophylla*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Phyllostomidae	*Lonchorhina*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Lophostoma*	0	0	0	0	0	0	0	0	0	0	1	1	30
Noctilionoidea	Phyllostomidae	*Macrophyllum*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Macrotus*	0	0	0	0	0	0	0	0	0	0	1	1	87, 119
Noctilionoidea	Phyllostomidae	*Mesophylla*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Micronycteris*	0	0	0	0	0	0	0	0	0	0	1	1	24, 30
Noctilionoidea	Phyllostomidae	*Mimon*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Phyllostomidae	*Monophyllus*	0	0	0	0	0	0	0	0	0	0	1	1	87, 119
Noctilionoidea	Phyllostomidae	*Musonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Neonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Phylloderma*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Phyllonycteris*	0	0	0	0	0	0	0	0	0	0	1	1	87, 119

Noctilionoidea	Phyllostomidae	*Phyllops*	0	0	0	0	0	0	0	0	0	0	1	1	130
Noctilionoidea	Phyllostomidae	*Phyllostomus*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Phyllostomidae	*Platalina*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Platyrrhinus*	0	0	0	0	0	0	0	0	0	0	1	1	24
Noctilionoidea	Phyllostomidae	*Pygoderma*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Rhinophylla*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Scleronycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Sphaeronycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Stenoderma*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Sturnira*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Tonatia*	0	0	0	0	0	0	0	0	1	1	1	1	18, 24
Noctilionoidea	Phyllostomidae	*Trachops*	0	0	0	0	0	0	0	0	0	0	1	1	30
Noctilionoidea	Phyllostomidae	*Trinycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Uroderma*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Vampyressa*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Vampyrodes*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Phyllostomidae	*Vampyrum*	0	0	0	0	0	0	0	0	0	0	0	1	
Noctilionoidea	Thyropteridae	*Thyroptera*	0	0	0	0	0	0	0	0	1	1	1	1	18
Pteropodidae	Pteropodidae	*†Propotto*	0	0	0	0	0	0	0	1	0	0	0	0	11, 140
Pteropodidae	Pteropodidae	*Acerodon*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Aethalops*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Alionycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Aproteles*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Balionycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Casinycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Chironax*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Cynopterus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Dobsonia*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Dyacopterus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Eidolon*	0	0	0	0	0	0	0	0	0	0	1	1	141
Pteropodidae	Pteropodidae	*Eonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Epomophorus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Epomops*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Haplonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Harpyionycteris*	0	0	0	0	0	0	0	0	0	0	0	1	

Table 2 (continued)

Superfamily	Family	Genus	Eo				Oligo		Mio				P-P	Rec	Source
			Ypr	Lut	Bart	Pria	Rup	Chat	Aqui	Burd	M Mio	L Mio	P-P	Rec	
		Ma:	55.8	48.6	40.4	37.2	33.9	28.4	23.0	20.4	16.0	11.6	5.3	0.012	
Pteropodidae	Pteropodidae	*Hypsignathus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Latidens*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Lissonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Macroglossus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Megaerops*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Megaloglossus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Melonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Micropteropus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Myonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Nanonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Neopteryx*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Notopteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Nyctimene*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Otopteropus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Paranyctimene*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Penthetor*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Plerotes*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Ptenochirus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Pteralopex*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Pteropus*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Rousettus*	0	0	0	0	0	0	0	0	0	0	1	1	104
Pteropodidae	Pteropodidae	*Scotonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Sphaerias*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Styloctenium*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Syconycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Pteropodidae	Pteropodidae	*Thoopterus*	0	0	0	0	0	0	0	0	0	0	0	1	
Rhinolophoidea	Craseonycteridae	*Craseonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Rhinolophoidea	Hipposideridae	*†Archerops*	0	0	0	0	0	0	0	1	0	0	0	0	55
Rhinolophoidea	Hipposideridae	*†Brevipalatus*	0	0	0	0	0	0	0	1	0	0	0	0	54, 55
Rhinolophoidea	Hipposideridae	*†Miophyllorhina*	0	0	0	0	0	0	0	1	0	0	0	0	50

Rhinolophoidea	Hipposideridae	*†Palaeophyllophora*	0	0	1	1	1	1	0	0	0	0	0	0	35
Rhinolophoidea	Hipposideridae	*†Paraphyllophora*	0	0	0	1	0	0	0	0	0	0	0	0	101
Rhinolophoidea	Hipposideridae	*†Riversleigha*	0	0	0	0	0	0	0	1	0	0	0	0	52
Rhinolophoidea	Hipposideridae	*†Vaylatsia*	0	0	0	1	1	1	0	0	0	0	0	0	55, 114, 120, 139
Rhinolophoidea	Hipposideridae	*†Xenorhinos*	0	0	0	0	0	0	0	1	0	0	0	0	53
Rhinolophoidea	Hipposideridae	*Anthops*	0	0	0	0	0	0	0	0	0	0	0	1	
Rhinolophoidea	Hipposideridae	*Asellia*	0	0	0	0	0	0	0	1	1	1	1	1	37, 74, 77, 126
Rhinolophoidea	Hipposideridae	*Aselliscus*	0	0	0	0	0	0	0	0	0	0	0	1	
Rhinolophoidea	Hipposideridae	*Cloeotis*	0	0	0	0	0	0	0	0	0	0	0	1	
Rhinolophoidea	Hipposideridae	*Coelops*	0	0	0	0	0	0	0	0	0	0	0	1	
Rhinolophoidea	Hipposideridae	*Hipposideros*	0	0	1	1	1	1	1	1	1	1	1	1	4, 11, 35, 47, 49, 51, 55, 69, 77, 104, 108, 110, 117, 118, 126, 141, 151, 152
Rhinolophoidea	Hipposideridae	*Paracoelops*	0	0	0	0	0	0	0	0	0	0	0	1	
Rhinolophoidea	Hipposideridae	*Rhinonicteris*	0	0	0	0	0	0	0	1	1	1	1	1	51
Rhinolophoidea	Hipposideridae	*Triaenops*	0	0	0	0	0	0	0	0	0	0	1	1	104
Rhinolophoidea	?Megadermatidae	*†Necromantis*	0	1	1	1	0	0	0	0	0	0	0	0	82
Rhinolophoidea	Megadermatidae	*†Saharaderma*	0	0	0	1	0	0	0	0	0	0	0	0	44
Rhinolophoidea	Megadermatidae	*Cardioderma*	0	0	0	0	0	0	0	0	0	0	1	1	10
Rhinolophoidea	Megadermatidae	*Lavia*	0	0	0	0	0	0	0	0	0	0	0	1	
Rhinolophoidea	Megadermatidae	*Macroderma*	0	0	0	0	0	0	0	0	1	1	1	1	45, 48, 90
Rhinolophoidea	Megadermatidae	*Megaderma*	0	0	0	0	0	1	1	1	1	1	1	1	37, 39, 108, 109, 110, 112, 126, 135, 151, 152
Rhinolophoidea	Rhinolophidae	*†Palaeonycteris*	0	0	0	0	0	0	0	1	0	0	0	0	44
Rhinolophoidea	Rhinolophidae	*Rhinolophus*	0	0	0	1	1	1	1	1	1	1	1	1	1, 3, 4, 35, 37, 60, 69, 71, 73, 74, 93, 107, 108, 109, 126, 134, 137, 151, 152
Rhinolophoidea	Rhinopomatidae	*†Qarunycteris*	0	0	0	1	0	0	0	0	0	0	0	0	44
Rhinolophoidea	Rhinopomatidae	*Rhinopoma*	0	0	0	0	0	0	0	0	0	1	1	1	67
Vespertilionoidea	†Philisidae	*†Dizzya*	1	0	0	0	0	0	0	0	0	0	0	0	115
Vespertilionoidea	†Philisidae	*†Philisis*	0	0	0	0	1	0	0	0	0	0	0	0	118
Vespertilionoidea	†Philisidae	*†Scotophilisis*	0	0	0	0	0	0	0	1	0	0	0	0	66, 142
Vespertilionoidea	†Philisidae	*†Vampyravus*	0	0	0	0	1	0	0	0	0	0	0	0	113, 120
Vespertilionoidea	†Philisidae	*†Witwatia*	0	0	0	1	0	0	0	0	0	0	0	0	44

Table 2 (continued)

Superfamily	Family	Genus	Eo				Oligo		Mio				P-P	Rec	Source
		Ma:	Ypr 55.8	Lut 48.6	Bart 40.4	Pria 37.2	Rup 33.9	Chat 28.4	Aqui 23.0	Burd 20.4	M Mio 16.0	L Mio 11.6	P-P 5.3	Rec 0.012	
Vespertilionoidea	Miniopteridae	*Miniopterus*	0	0	0	0	0	0	0	0	1	1	1	1	1, 4, 60, 71, 93, 107, 126, 145, 152
Vespertilionoidea	Molossidae	*†Cuvierimops*	0	0	0	1	1	1	0	0	0	0	0	0	42, 78
Vespertilionoidea	Molossidae	*†Petramops*	0	0	0	0	0	0	0	0	1	0	0	0	46
Vespertilionoidea	Molossidae	*†Potamops*	0	0	0	0	0	0	0	0	1	0	0	0	18, 23
Vespertilionoidea	Molossidae	*†Wallia*	0	0	1	1	0	0	0	0	0	0	0	0	28, 128
Vespertilionoidea	Molossidae	*Chaerephon*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Cheiromeles*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Cynomops*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Eumops*	0	0	0	0	0	0	0	0	1	1	1	1	18, 21, 23, 24, 101
Vespertilionoidea	Molossidae	*Molossops*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Molossus*	0	0	0	0	0	0	0	0	0	0	1	1	24
Vespertilionoidea	Molossidae	*Mops*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Mormopterus*	0	0	0	0	0	0	1	1	1	1	1	1	18, 23, 78, 126
Vespertilionoidea	Molossidae	*Myopterus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Nyctinomops*	0	0	0	0	0	0	0	0	0	0	1	1	22, 24
Vespertilionoidea	Molossidae	*Otomops*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Platymops*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Promops*	0	0	0	0	0	0	0	0	0	0	1	1	24
Vespertilionoidea	Molossidae	*Sauromys*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Molossidae	*Tadarida*	0	0	0	1	1	1	1	1	1	1	1	1	1, 2, 24, 29, 35, 78, 87, 88, 107, 109, 126
Vespertilionoidea	Molossidae	*Tomopeas*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Natalidae	*†Honrovits*	1	0	0	0	0	0	0	0	0	0	0	0	7
Vespertilionoidea	Natalidae	*†Primonatalus*	0	0	0	0	0	0	0	1	0	0	0	0	87
Vespertilionoidea	Natalidae	*Chilonatalus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Natalidae	*Natalus*	0	0	0	0	0	0	0	0	0	0	1	1	24, 87
Vespertilionoidea	Natalidae	*Nyctiellus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*†Ancenycteris*	0	0	0	0	0	0	0	0	1	0	0	0	131
Vespertilionoidea	Vespertilionidae	*†Anzanycteris*	0	0	0	0	0	0	0	0	0	0	1	0	15, 28, 143

Vespertilionoidea	Vespertilionidae	*†Chamtwaria*	0	0	0	0	0	0	0	1	0	0	0	0	11
Vespertilionoidea	Vespertilionidae	*†Hanakia*	0	0	0	0	0	1	1	1	0	0	0	0	65
Vespertilionoidea	Vespertilionidae	*†Karstala*	0	0	0	0	0	0	0	1	0	0	0	0	25
Vespertilionoidea	Vespertilionidae	*†Khonsunycteris*	0	0	0	1	0	0	0	0	0	0	0	0	44
Vespertilionoidea	Vespertilionidae	*†Miomyotis*	0	0	0	0	0	0	0	1	0	0	0	0	75
Vespertilionoidea	Vespertilionidae	*†Miostrellus*	0	0	0	0	0	0	0	0	1	0	0	0	65, 126
Vespertilionoidea	Vespertilionidae	*†Oligomyotis*	0	0	0	0	1	0	0	0	0	0	0	0	5, 38
Vespertilionoidea	Vespertilionidae	*†Paleptesicus*	0	0	0	0	0	0	0	0	1	1	0	0	126, 149, 150, 152
Vespertilionoidea	Vespertilionidae	*†Pleistomyotis*	0	0	0	0	0	0	0	0	0	0	1	0	148
Vespertilionoidea	Vespertilionidae	*†Plionycteris*	0	0	0	0	0	0	0	0	0	0	1	0	80
Vespertilionoidea	Vespertilionidae	*†Potamonycteris*	0	0	0	0	0	0	0	0	1	0	0	0	20
Vespertilionoidea	Vespertilionidae	*†Quinetia*	0	0	0	0	1	0	0	0	0	0	0	0	65, 96
Vespertilionoidea	Vespertilionidae	*†Samonycteris*	0	0	0	0	0	0	0	0	0	1	0	0	101, 126
Vespertilionoidea	Vespertilionidae	*†Shanwangia*	0	0	0	0	0	0	0	0	1	0	0	0	147
Vespertilionoidea	Vespertilionidae	*†Simonycteris*	0	0	0	0	0	0	0	0	0	0	1	0	20, 125
Vespertilionoidea	Vespertilionidae	*†Stehlinia*	0	1	1	1	1	1	0	0	0	0	0	0	35, 82, 100, 111
Vespertilionoidea	Vespertilionidae	*†Suaptenos*	0	0	0	0	0	0	0	1	0	0	0	0	75
Vespertilionoidea	Vespertilionidae	*†Submyotodon*	0	0	0	0	0	0	0	0	1	0	0	0	152
Vespertilionoidea	Vespertilionidae	*Antrozous*	0	0	0	0	0	0	0	0	1	1	1	1	28, 33, 132
Vespertilionoidea	Vespertilionidae	*Arielulus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Barbastella*	0	0	0	0	0	0	0	0	0	0	1	1	72, 107
Vespertilionoidea	Vespertilionidae	*Bauerus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Chalinolobus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Cistugo*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Corynorhinus*	0	0	0	0	0	0	0	0	0	1	1	1	58, 138, 139
Vespertilionoidea	Vespertilionidae	*Eptesicus*	0	0	0	0	0	0	0	1	1	1	1	1	3, 14, 21, 24, 30, 32, 33, 61, 70, 72, 79, 87, 92, 95, 107, 130, 137, 151, 152
Vespertilionoidea	Vespertilionidae	*Euderma*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Eudiscopus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Falsistrellus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Glauconycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Glischropus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Harpiocephalus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Hesperoptenus*	0	0	0	0	0	0	0	0	0	0	0	1	

Table 2 (continued)

Superfamily	Family	Genus	Eo				Oligo		Mio				P-P	Rec	Source
		Ma:	Ypr 55.8	Lut 48.6	Bart 40.4	Pria 37.2	Rup 33.9	Chat 28.4	Aqui 23.0	Burd 20.4	M Mio 16.0	L Mio 11.6	P-P 5.3	Rec 0.012	
Vespertilionoidea	Vespertilionidae	*Histiotus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Hypsugo*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Ia*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Idionycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Kerivoula*	0	0	0	0	0	0	0	0	0	0	1	1	16, 64
Vespertilionoidea	Vespertilionidae	*Laephotis*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Lasionycteris*	0	0	0	0	0	0	0	0	0	0	1	1	32
Vespertilionoidea	Vespertilionidae	*Lasiurus*	0	0	0	0	0	0	0	0	0	1	1	1	21, 27, 32, 41, 62, 132
Vespertilionoidea	Vespertilionidae	*Mimetillus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Murina*	0	0	0	0	0	0	0	0	0	0	1	1	72, 94
Vespertilionoidea	Vespertilionidae	*Myotis*	0	0	0	0	0	1	1	1	1	1	1	1	1, 3, 5, 17, 19, 24, 27, 35, 40, 58, 60, 69, 71, 72, 73, 93, 94, 95, 101, 107, 110, 126, 136, 137, 144, 151, 152
Vespertilionoidea	Vespertilionidae	*Neoromicia*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Nyctalus*	0	0	0	0	0	1	1	1	1	1	1	1	65, 107
Vespertilionoidea	Vespertilionidae	*Nycticeinops*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Nycticeius*	0	0	0	0	0	0	0	0	0	0	1	1	12
Vespertilionoidea	Vespertilionidae	*Nyctophilus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Otonycteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Parastrellus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Perimyotis*	0	0	0	0	0	0	0	0	0	0	1	1	85, 98
Vespertilionoidea	Vespertilionidae	*Pharotis*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Philetor*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Phoniscus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Pipistrellus*	0	0	0	0	0	0	0	0	0	1	1	1	12, 95, 107, 109, 137
Vespertilionoidea	Vespertilionidae	*Plecotus*	0	0	0	0	0	0	0	0	1	1	1	1	60, 70, 72, 73, 85, 95, 107, 139, 152
Vespertilionoidea	Vespertilionidae	*Rhogeesa*	0	0	0	0	0	0	0	0	0	0	1	1	30

Vespertilionoidea	Vespertilionidae	*Scoteanax*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Scotoecus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Scotomanes*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Scotophilus*	0	0	0	0	0	0	0	0	1	1	1	1	9, 36
Vespertilionoidea	Vespertilionidae	*Scotorepens*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Scotozous*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Tylonicteris*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Vespadelus*	0	0	0	0	0	0	0	0	0	0	0	1	
Vespertilionoidea	Vespertilionidae	*Vespertilio*	0	0	0	0	0	0	0	0	1	1	1	1	37, 102

1: Aguilar et al. 1984; **2**: Arroyo-Cabrales et al. 2002; **3**: Avery 1998; **4**: Avery 2003; **5**: Bailey 2004; **6**: Barghoorn 1977; **7**: Beard et al. 1992; **8**: BiochroM'97 1997; **9**: Black and Krishtalka 1986; **10**: Butler 1978; **11**: Butler and Hopwood 1957; **12**: Butler and Greenwood 1965; **13**: Butler 1984; **14**: Cahn 1939; **15**: Cassiliano 1999; **16**: Čermák et al. 2007; **17**: Choate and Hall 1967; **18**: Cozzuol 2006; **19**: Czaplewski 1987; **20**: Czaplewksi 1991; **21**: Czaplewski 1993; **22**: Czaplewski 1996; **23**: Czaplewski 1997; **24**: Czaplewksi and Cartelle 1998; **25**: Czaplewski and Morgan 2000; **26**: Czaplewski and Peachey 2003; **27**: Czaplewski et al. 1999; **28**: Czaplewski et al. 2008; **29**: Czaplewski et al. 2003a; **30**: Czaplewski et al. 2005; **31**: Czaplewski et al. 2003b; **32**: Dalquest 1978; **33**: Dalquest 1983; **34**: Dalquest and Roth 1970; **35**: de Bonis et al. 1973; **36**: Engesser 1972; **37**: Engesser and Ziegler 1996; **38**: Galbreath 1962; **39**: Ginsburg 1963; **40**: Godawa 1993; **41**: Grady and Olson 2006; **42**: Gunnell and Simmons 2005; **43**: Gunnell et al. 2003; **44**: Gunnell et al. 2008; **45**: Hand 1985; **46**: Hand 1990; **47**: Hand 1993; **48**: Hand 1996; **49**: Hand 1997a; **50**: Hand 1997b; **51**: Hand 1997c; **52**: Hand 1998a; **53**: Hand 1998b; **54**: Hand and Archer 2005; **55**: Hand and Kirsch 2003; **56**: Hand et al. 1998; **57**: Hand et al. 1994; **58:** Handley 1959; **59**: Heller 1935; **60**: Heller 1936; **61**: Hendey 1981; **62**: Hibbard 1950; **63**: Hooker 1996; **64**: Horáček 1986; **65**: Horáček 2001; **66**: Horáček et al. 2006; **67**: Hulva et al. 2007; **68**: Jepsen 1966; **69**: Jin et al. 2000; **70**: Kormos 1930; **71**: Kowalski 1956; **72**: Kowalski 1962a; **73**: Kowalski 1962b; **74**: Lavocat 1961; **75**: Lawrence 1943; **76**: Legendre 1980; **77**: Legendre 1982; **78**: Legendre 1985; **79**: Lemon and Churcher 1961; **80**: Lindsay and Jacobs 1985; **81**: Maitre et al. 2008; **82**: Marandat et al. 1993; **83**: Meschinelli 1903; **84**: Morgan 1989; **85**: Morgan 1991; **86**: Morgan and Czaplewski 1999; **87**: Morgan and Czaplewski 2003; **88**: Morgan and Ridgeway 1987; **89**: Morgan et al. 1988; **90**: Myers et al. 2001; **91**: Ostrander 1983; **92**: Pocock 1987; **93**: Popov 2004; **94**: Qiu and Storch 2000; **95**: Qiu et al. 1985; **96**: Quinet 1965; **97**: Rana et al. 2005; **98**: Ray 1967; **99**: Revilliod 1917; **100**: Revilliod 1919; **101**: Revilliod 1922; **102**: Rossina et al. 2006; **103**: Russell et al. 1973; **104**: Samonds 2007; **105**: Savage 1951; **106**: Savage and Russell 1983; **107**: Sevilla 1989; **108**: Sevilla 1990; **109**: Sevilla 1991; **110**: Sigé 1968; **111**: Sigé 1974; **112**: Sigé 1976; **113**: Sigé 1985; **114**: Sigé 1990; **115**: Sigé 1991; **116**: Sigé and Russell 1980; **117**: Sigé et al. 1982; **118**: Sigé et al. 1994; **119**: Silva-Taboada 1974; **120**: Simmons and Geisler 1998; **121**: Simmons et al. 2008; **122**: Smith and Storch 1981; **123**: Smith and Russell 1992; **124**: Smith et al. 2007; **125**: Stirton 1931; **126**: Storch 1999; **127**: Storch et al. 2002; **128**: Storer 1984; **129**: Strand 1928; **130**: Suárez and Díaz-Franco 2003; **131**: Sutton and Genoways 1974; **132**: Thewissen and Smith 1987; **133**: Tong 1997; **134**: Topál 1963; **135**: Topál 1974; **136**: Topál 1983; **137**: Topál 1985; **138**: Topál 1989a; **139**: Topál 1989b; **140**: Walker 1969; **141**: Wesselmann 1984; **142**: Wessels et al. 2003; **143**: White 1969; **144**: Wilson 1968; **145**: Wołoszyn 1986; **146**: Worthy and Holdaway 1994; **147**: Yang 1977; **148**: Yoon et al. 1984; **149**: Zapfe 1950; **150**: Zapfe 1970; **151**: Ziegler 2003; **152**: Ziegler 1994

Appendix 2

Statistical calculations for Vespertilionoidea, following the method of Foote and Raup (1996).

Using the data for all vespertilionoid bats (Appendix 1), we first computed the total number of temporal bins in which each genus occurs. There are 11 stratigraphic bins (excluding the Recent), beginning with the Ypresian (early Eocene) and ending with the Plio-Pleistocene. Of the 56 vespertilionoid genera that occur as fossils, 38 occur in only one bin, five range through two bins, eight occur in three bins, one occurs in four bins, two occur in five bins, and one each occurs in six (*Myotis*) and eight (*Tadarida*) bins. No vespertilionoid bats lasted exactly seven bins, or in any more than eight bins.

To estimate preservation probability, *R*, we calculate the *FreqRat* (which estimates *R*) following the formula:

$$R \approx FreqRat = f(2)^2 \Big/ [f(1)f(3)]$$

where *f(x)* is the frequency of genera with observed range-durations of *x* bins. For Vespertilionoidea, $R \approx FreqRat = 5^2 / [(38)(8)] = 0.082$.

To account for differential original temporal distributions of bat genera, *R* must be scaled according to original durations. Estimated preservation probability is used to calculate an estimate of the probability $P_1(T)$ that a taxon is preserved at least once given a true original duration *T*. The probability that a genus with original duration *T* is not at all preserved equals $(1\text{-}R)^T$. Thus, the probability that it is preserved at least once equals:

$$P_1(T) = 1 - (1 - R)^T$$

For example, to calculate the probability that a genus is preserved given a true original duration of three bins, the equation became $P_1(3) = 1 - (1 - 0.082)^3 = 0.0227$. This same procedure was used for all possible values of *T* (i.e., *T*=1-∞, though in this and subsequent calculations it is usually sufficient to take out to just several hundred).

We next estimated extinction rate, *q*, which was to be used to compute original genus durations. We used linear regression on the ln-transformed frequencies of genera with a range of two or more bins. The slope of the linear regression line equals *q* (the extinction rate) with the sign reversed. Next, original durations were calculated, assuming a constant extinction rate, *q*, and an exponential distribution of original durations. *q* was calculated from the ln-slope of range-frequencies (omitting taxa that occur in only one bin) as the slope with the sign reversed. For Vespertilionoidea, the ln-slope of range-frequency distributions is −0.3226, so the extinction rate *q* equals 0.3226.

Using our estimate for *q*, we calculated the probability, *h(T)*, that the original distribution equaled *T* as:

$$h(T) = e^{-q(T-1)} - e^{-qT}$$

Using *T* of 3 again, we see that $h(3) = e^{-(0.3226)(3-1)} - e^{-(.3226)(3)} = 0.145$. Again, this procedure was calculated for all values of *T*.

Finally, to calculate completeness, we computed the sum, for all original durations, *T*, of the product between *h(T)* (probability of having original duration *T*) and $P_1(T)$ (probability of being preserved at least once during an interval given an original duration *T*) as:

$$P_p = \sum_{T=1}^{\infty} h(T) P_1(T)$$

As *T* increased, the completeness for that number of bins decreases rapidly, so this summation was to only be taken to several hundred rows in a spreadsheet. Doing this for Vespertilionoidea to 900 rows gave a completeness of 24.5% (rounded and included in Table 1). Summing the completeness calculations up to only 50 rows produced the same overall completeness value (to eight digits), indicating that it is sufficient to compute the summation using a finite set of values for *T* that is substantially less than 1000.

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