Bat Systematics in the Light of Unconstrained Analyses of a Comprehensive Molecular Supermatrix

Lucila I. Amador, R. Leticia Moyers Arévalo, Francisca C. Almeida, Santiago A. Catalano & Norberto P. Giannini

Journal of Mammalian Evolution

ISSN 1064-7554

J Mammal Evol
DOI 10.1007/s10914-016-9363-8

Springer

J Mammal Evol
DOI 10.1007/s10914-016-9363-8

ORIGINAL PAPER

Bat Systematics in the Light of Unconstrained Analyses of a Comprehensive Molecular Supermatrix

Lucila I. Amador[1] · **R. Leticia Moyers Arévalo**[1] · **Francisca C. Almeida**[2] · **Santiago A. Catalano**[1,3] · **Norberto P. Giannini**[1,3,4]

Abstract Bats (Chiroptera) represent the largest diversification of extant mammals after rodents. Here we report the results of a large-scale phylogeny of bats based on unconstrained searches for a data matrix of 804 non-chimeric, taxonomically updated bat terminals (796 species represented by a single terminal plus three species represented by ≥2 genetically distinct subspecies), able to preliminary test the systematics of most groups simultaneously. We used nine nuclear and mitochondrial DNA sequence markers fragmentary represented for ingroups (c. 90% and 64% of extant diversity at genus and species level, respectively) and 20 diverse placental outgroups. Maximum Likelihood and Parsimony analyses applied to the concatenated dataset yielded a highly resolved, variously supported phylogeny that recovered the majority of currently recognized clades at all levels of the chiropteran tree. Calibration points based on 44 key fossils allowed the Bayesian dating of bat origins at c. 4 my after the K-Pg boundary, and the determination of stem and crown ages of intraordinal clades. As expected, bats appeared nested in Laurasiatheria and split into Yinpterochiroptera and Yangochiroptera. More remarkable, all polytypic, currently recognized families were monophyletic, including Miniopteridae, Cistugidae, and Rhinonycteridae, as well as most polytypic genera with few expected exceptions (e.g., *Hipposideros*). The controversial Myzopodidae appeared in a novel position as sister of Emballonuroidea—a result with interesting biogeographic implications. Most recently recognized subfamilies, genera, and species groups were supported or only minor adjustments to the current taxonomy would be required, except Molossidae, which should be revised thoroughly. In light of our analysis, current bat systematics is strongly supported at all levels; the emergent perception of a strong biogeographic imprint on many recovered bat clades is emphasized.

Keywords Chiroptera · Phylogeny · Molecular dating · Maximum likelihood · Parsimony

Introduction

With more than 1200 currently recognized species in 21 extant families, diversity of bats (Chiroptera) is only second to rodents among extant mammals (Simmons 2005). Today bats are thought to belong in a single, solidly established clade; however, in the recent past, bat monophyly was questioned, and in general bat systematics was controversial chiefly around four major topics. First, neurological data suggested that non-echolocating fruitbats (Megachiroptera: Pteropodidae) were related to primates and flying lemurs (or colugos; Dermoptera) instead of being related to echolocating bats (Microchiroptera), as traditionally accepted. This bat diphyly hypothesis (Pettigrew 1986, 1991a, 1991b) was rejected on the basis of mounting morphological evidence (reviewed in Simmons 1994) and by all subsequent molecular or combined phylogenetic analyses (Ammerman and Hillis 1992; Murphy et al. 2001; Springer

Electronic supplementary material The online version of this article (doi:10.1007/s10914-016-9363-8) contains supplementary material, which is available to authorized users.

✉ Norberto P. Giannini
ngiannini@amnh.org

[1] Unidad Ejecutora Lillo (UEL: FML-CONICET), Tucumán, Argentina

[2] Genética y Evolución de Buenos Aires (IEGEBA: UBA-CONICET), Instituto de Ecología, Buenos Aires, Argentina

[3] Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán (UNT), Tucumán, Argentina

[4] American Museum of Natural History (AMNH), Division of Vertebrate Zoology, Department of Mammalogy, NY, USA

Published online: 24 November 2016

et al. 2004; Meredith et al. 2011; dos Reis et al. 2012; O'Leary et al. 2013), which led to the conclusion that the historically recognized Chiroptera was among the most robustly supported clade of mammals, as anticipated by Simmons (1994). Second, these results also suggested that colugos may not be sister to bats in the clade Volitantia, grouping for which there was significant morphological evidence (Simmons 1994; Simmons and Geisler 1998; Gunnell and Simmons 2005), but to primates instead (Ammerman and Hillis 1992). Bats would not group with colugos, tree shrews, and primates in the classical supraordinal clade Archonta (Gregory 1910), but with laurasiatherians, a large clade of disparate mammals that also included lipothyphlan insectivores (shrews, moles, hedgehogs, and solenodons), pangolins, carnivorans, most ungulates, and cetaceans (Murphy et al. 2001; Springer et al. 2004; Meredith et al. 2011; O'Leary et al. 2013). Third, the new molecular data strongly suggested that echolocating bats (microbats) were not monophyletic. First shown by Hutcheon et al. (1998) on the basis of single-copy DNA hybridization, the fruit bat position was consistently recovered as sister to one group of microbats (currently known as rhinolophoids). Fruit bats nested within microbats in most successive analyses (e.g., Teeling et al. 2000, 2005, 2012; Eick et al. 2005; Tsagkogeorga et al. 2013). Fourth, this arrangement revealed that several bat taxa (families and genera) had rather unexpected relationships so the then accepted intraordinal classification, the one proposed by Koopman (1993), needed revision. For instance, Kirsch et al. (1998) first suggested noctilionoid (instead of nataloid) relationships for the New Zealand endemic Mystacinidae, and recently Hoofer and Van Den Bussche (2003) and Lack et al. (2010), respectively, recognized new monotypic families to successively segregate *Miniopterus* and *Cistugo* from the large Vespertilionidae.

Remarkable progress has been made in resolving the phylogeny of almost all polytypic bat families. Examples include Pteropodidae (Giannini and Simmons 2003, 2005; Giannini et al. 2006, 2008, 2009; Esselstyn et al. 2008; Almeida et al. 2009, 2011, 2016; Nesi et al. 2013; Hassanin 2014); Vespertilionidae (Hoofer and Van Den Bussche 2003; Lack and Van Den Bussche 2010; Roehrs et al. 2010; Juste et al. 2013; Ruedi et al. 2013); Phyllostomidae (Baker et al. 2003, 2012; Datzmann et al. 2010; Dumont et al. 2011; Rojas et al. 2016); Molossidae (Ammerman et al. 2012; Gregorin and Cirranello 2015); Mormoopidae (Simmons and Conway 2001; Van Den Bussche et al. 2002; Dávalos 2006; Thoisy et al. 2014); Emballonuridae (Lim et al. 2008; Goodman et al. 2012; Ruedi et al. 2012); Natalidae (Dávalos 2005; Tejedor 2011); Rhinolophidae (Guillén-Servent et al. 2003; Stoffberg et al. 2010; Foley et al. 2015; Bailey et al. 2016). Also, the phylogeny of speciose genera has been resolved to a significant degree of coverage; e.g., *Myotis* (Stadelmann et al. 2007; Larsen et al. 2012; Ruedi et al. 2013); *Pteropus* (Giannini et al. 2008; O'Brien et al. 2009; Almeida et al. 2014); *Rhinolophus* (Guillén-Servent et al. 2003; Zhou et al. 2009; Stoffberg et al. 2010); *Hipposideros* (Murray et al. 2012; Thong et al. 2012a, 2012b); *Artibeus* (Lim et al. 2004; Redondo et al. 2008); *Sturnira* (Velazco and Patterson 2013). Systematic research in bats also made progress with the accelerated pace of new species discoveries (e.g., *Xeronycteris vierai* Gregorin and Ditchfield 2005; *Hipposideros khaokhouayensis* Guillén-Servent and Francis 2006; *Desmalopex microleucopterus* Esselstyn et al. 2008; *Myotis phanluongi* Borisenko et al. 2008; *Rhinolophus xinanzhougguoensis* Zhou et al. 2009; *Glischropus bucephalus* Csorba 2011; *Dryadonycteris capixaba* Nogueira et al. 2012; *Myotis indochinensis* Son et al. 2013; *Histiotus diaphanopterus* Feijó et al. 2015).

As a result of this volume of phylogenetic research, a wealth of phylogenetic data became available for bats as a group. Particularly, DNA sequence data allowed the compilation of large data matrices for phylogenetic analyses at unprecedented levels of both taxonomic and character sampling. Higher-level relationships were tested with ever-increasing character samples (Teeling et al. 2000, 2005, 2009; Eick et al. 2005; Tsagkogeorga et al. 2013; Foley et al. 2015; Bailey et al. 2016) with the result of firmly establishing the backbone structure of the chiropteran tree, depicted in Fig. 1. However, these analyses had characteristically low taxonomic coverage, with representatives of all bat families but very few bat species (range 9–30 terminals).

There is now ample consensus that results of phylogenetic analyses are improved with both denser taxon (Zwickl and Hillis 2002; Havird and Miyamoto 2010; Pick et al. 2010; Vahtera et al. 2013) and comprehensive character sampling (e.g., Meredith et al. 2011; O'Leary et al. 2013). Two recent efforts approached the chiropteran phylogeny from the perspective of covering a comprehensive taxonomic sampling. First, Agnarsson et al. (2011) produced a phylogeny of 648 terminals representing at least 550 species based on the sequence of the mitochondrial gene cytochrome b (cyt-b). The cyt-b had a remarkable performance at various phylogenetic levels including Chiroptera, Megachiroptera, most bat families, genera, and numerous intrageneric groupings, thus demonstrating the value of this marker for bat (and mammalian) systematics. Discussing major clades in particular, unexpected groupings in Agnarsson et al. (2011) included a monophyletic Microchiroptera (seldom recovered with molecular data), Miniopteridae as sister of Noctilionoidea (instead of sister of Cistugidae + Vespertilionidae), Mystacinidae + Thyropteridae nested deeply inside Noctilionoidea (instead of near the base of the superfamily), Myzopodidae and Emballonuridae associated with Vespertilionoidea, as well as the paraphyly of widely accepted families (Mormoopidae and Emballonuridae). The second study, by Shi and Rabosky (2015), covered 812 bat terminals with fragmentary sequence representation from 29 loci. This study aimed at generating a taxonomically dense phylogeny for the purpose of estimating evolutionary diversification rates

in Chiroptera. These authors used a backbone constraint that forced the monophyly of several major clades during tree search based on groups from Teeling et al. (2005; see our Fig. 1); specifically, this backbone included the Yangochiroptera and Yinpterochiroptera suborders, the "microbat" superfamilies Rhinolophoidea, Emballonuroidea, Noctilionoidea, and Vespertilionoidea, and the large subfamily Myotinae in Vespertilionidae (Shi and Rabosky 2015). The effect of such major restrictions were noted for instance in Yangochiroptera, where the position of the Malagasy endemic *Myzopoda* was inforced as sister of Noctilionoidea (as in Teeling et al. 2005), when alternative positions were also possible (see Eick et al. 2005; Meredith et al. 2011). In spite of these constraints, or because of them, Shi and Rabosky (2015) achieved a remarkable phylogenetic result demonstrated in the number and importance of supported clades recovered at all levels; however, their goals were not systematic and so the relevance of a species-level, taxonomically dense phylogeny of bats remained largely unassessed. Considering that their results cannot be used to test the relationships among the main lineages of bats, and that the constraints may have also affected the recovered branching pattern within these lineages, an unconstrained analysis of similar scale would be necessary to properly test the phylogenetic relationships within Chiroptera.

Comprehensive phylogenies are important because they allow to simultaneously test all historically relevant systematic hypotheses, eventually discovering new relationships that only emerge with the unrestricted interaction of diverse data. In addition, the resulting phylogenetic hypotheses are extremely useful as framework to study macroevolutionary aspects of groups, such as diversification hypotheses (e.g., Fabre et al. 2012; Shi and Rabosky 2015), character evolution (e.g., O'Leary et al. 2013), or evolution of life history strategies (e.g., Wilkinson and South 2002). Previous results

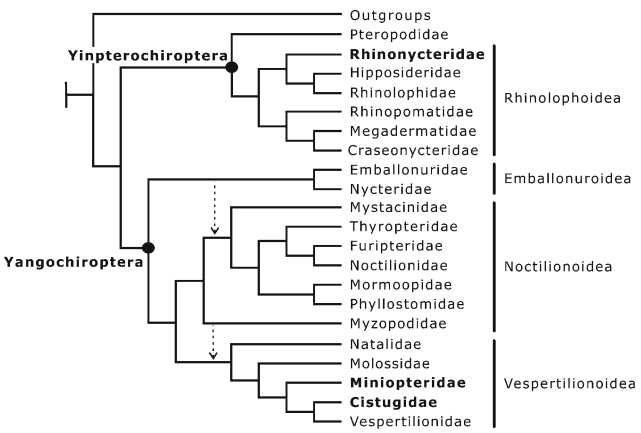

Fig. 1 Current hypothesis of intraordinal relationships in Chiroptera, modified from Teeling et al. (2005). Families in bold correspond to the recent recognized families according to Foley et al. (2015), Lack et al. (2010), and Hoofer and Van Den Bussche (2003). Dashed arrows showed the alternative positions for Emballonuroidea and Myzopodidae recovered by Meredith et al. (2011)

(Agnarsson et al. 2011; Shi and Rabosky 2015) suggested that a comprehensive, species-rich phylogeny of bats is within reach. Here we attempt to provide such a phylogeny with an unconstrained analysis, of a wide taxonomically updated sample, without chimeric terminals, based on a depurated molecular sampling. Our specific goals were: 1) to assess the phylogenetic relationships among extant bat lineages and determine the level of resolved structure that is possible to recover without search constraints; 2) to evaluate the status of current chiropteran systematics in one analysis, simultaneously from outgroups to bat species, on the basis of this comprehensive taxonomic and character coverage; and 3) to provide a dated chiropteran tree on the basis of as many uncontroversial fossil calibration points as possible.

We show that previously used backbone constraints precluded the discovery of potential new groups and were unnecessary given the accuracy and fidelity of phylogenetic reconstruction at all systematics levels obtained in the present unconstrained analysis. We recovered a highly resolved, highly supported phylogeny of bats, in agreement with most of the current understanding of chiropteran systematics, which shows extraordinary strength in face of hard tests such as the analyses that we applied. The resulting topology becomes available for further studies, and demonstrate the fact that, as in other groups (e.g., rodents; Fabre et al. 2012), analyses of carefully compiled super-matrices reveal phylogenetic structure that emerges purely from data interactions, without the need of neither controversial supertree strategies, nor massive backbone constraints. In addition we show that while the fossil record of bats is demonstrably empoverished with respect to expected diversity (see Eiting and Gunnell 2009), this record did allow for a solid dating of the chiropteran tree when many fossils were considered. We evaluated the systematic relevance of the recent advances in phylogenetics at all levels of Chiroptera in the light of our results based on unconstrained analyses of large supermatrices.

Materials and Methods

Taxonomic Sampling

We built a data matrix that included 799 currently recognized species following Simmons (2005) and other authorities (e.g., Velazco 2005; Redondo et al. 2008; Solari et al. 2009; Datzmann et al. 2010; Lack et al. 2010; Roehrs et al. 2010; Juste et al. 2013; Ruedi et al. 2013; see Table SI.1 for included species recognized after Simmons 2005, Supplementary Information), plus eight genetically distinct subspecies classified into three of these species. This matrix included all the species and subspecies represented in the GenBank database as of March 2015 (see taxonomic list and accession numbers in Table SI.2) for the gene sequences selected for this study (see

below). All 21 currently recognized bat families were represented, i.e., the 18 traditional bat families plus Cistugidae and Miniopteridae, as separated from Vespertillionidae (see Lack et al. 2010 and Hoofer and Van Den Bussche 2003, respectively), and Rhinonycteridae as separated from Hipposideridae (Foley et al. 2015; see Table 1). Twenty taxa from diverse placental orders were added as outgroups: *Dasypus novemcinctus* (Xenarthra), *Choloepus hoffmani* (Xenarthra), *Elephantulus edwardii* (Macroscelidea), *Chrysochloris asiatica* (Afrosoricida), *Capra hircus* (Artiodactyla), *Equus caballus* (Perissodactyla), *Erinaceus europaeus* (Lipotyphla), *Galeopterus variegatus* (Dermoptera), *Homo sapiens* (Primates), *Loxodonta africana* (Proboscidea), *Manis pentadactyla* (Pholidota), *Mus musculus* (Rodentia), *Mustela putorius* (Carnivora), *Ochotona princeps* (Lagomorpha), *Orycteropus afer* (Tubulidentata), *Procavia capensis* (Hyracoidea), *Sorex araneus* (Lipotyphla), *Trichechus manatus* (Sirenia), *Tupaia belangeri* (Scandentia), and *Tursiops truncatus* (Cetacea). Thereby the analysis comprised a total of 824 terminals.

Characters and Matrix Compilation

Molecular data selection began with the premise of compiling DNA sequences that were represented in at least 100 species, including outgroups. This search resulted in four mitochondrial and five nuclear genes (Table 2); mitochondrial genes included the cytochrome b (Cyt-*b*), the NADH dehydrogenase subunit 1 (ND1), and the ribosomal subunits 12S and 16S; nuclear genes included the dentin matrix protein 1 (DMP1), the recombination activating protein 1 (RAG1), the recombination activating protein 2 (RAG2), exon 11 of the breast cancer susceptibility protein 1 (BRCA1), and exon 28 of the von Willebrand factor (vWF). These sequences are of proven systematic utility in bats, and they have been generated and used in different combinations, by several previous authors (e.g., Baker et al. 2003; Giannini and Simmons 2003; Hoofer and Van Den Bussche 2003; Dávalos 2005; Teeling et al. 2005; Stadelmann et al. 2007; Hoffmann et al. 2008; Roehrs et al. 2010; Agnarsson et al. 2011; Ammerman et al. 2012; Ruedi et al. 2013; Almeida et al. 2014; Shi and Rabosky 2015, among many others). GenBank accession numbers are given in Table SI.2.

Sequences were compiled with the program GB2TNT ("GenBank-to-TNT" Goloboff and Catalano 2012), a pipeline for creating large molecular matrices that selects sequences included in GenBank files by using filters defined by the user. This program extracts the sequences from a GenBank file, creates a Fasta file, produces the alignment by calling an external program defined by the user, and generates a data matrix in TNT format (see Goloboff et al. 2008). Data files were then reformatted manually to be read in RAxML (Stamatakis et al. 2008).

The main premise followed during the matrix generation was to maintain a high level of curation. Hence the matrix was depurated following several criteria. To the extent possible, dubious sequences, identified by equivocal positions in exploratory phylogenetic analyses, and / or by seemingly artifactual alignments (e.g., unexpectedly long internal gaps), were discarded or replaced (when available). Sequences resulting from shotgun sequencing strategy were not included. We avoided taxon duplication, correcting both taxonomic (e.g., synonymies) and syntactic (e.g., ambiguities in species entries) inaccuracies. The cases of taxonomic revalidations (cryptic species derived from an accepted taxon) were carefully considered, including only the sequences published after the recognition of the new species. No subspecies were considered, except in the cases in which the taxa were recently elevated as species, or when no sequence from the type species was available.

The selected sequences of each marker were aligned separately using the program MAFFT version 7 (Katoh and Standley 2013) with default settings. Then, the coding gene alignments were edited using Mesquite (version 3.03, Maddison and Maddison 2015) to make sure they were all in frame, while the mitochondrial 12S and 16S genes were trimmed using Gblocks (version 0.91b, Castresana 2002; Talavera and Castresana 2007) to remove regions with complex alignment. In all analyses (see below), indels were treated as missing data. The xenarthran *Dasypus novemcinctus* was designated to root the trees. In a few individual-gene analyses that lacked *Dasypus* sequences, another basal placental outgroup taxon was selected to root the tree.

In addition to these nine markers, we compiled sequences from the mitochondrial gene COI. This marker is of extended use in bats as barcoding tool (e.g., Clare et al. 2007; Kruskop et al. 2012; Wilson et al. 2014) and also in phylogenetic analyses (e.g., Shi and Rabosky 2015). However, in this study, preliminary phylogenetic analysis showed that the compiled COI sequences lacked phylogenetic structure whatsoever in the individual-gene analysis, and destroyed all the recovered structure in both the mitochondrial and combined (mitochondrial + nuclear) phylogenetic analyses (see below). It is likely that imposing constraints on the topology may affect positively the performance of this important marker (e.g., Shi and Rabosky 2015); because here we did not enforce constraints on any group, we did not include the marker and suggest that COI data be analyzed in more detail in future contributions.

Phylogenetic Analyses

We conducted two series of unconstrained phylogenetic analyses with different optimality criteria. First, we performed a maximum likelihood (ML) analysis on the total dataset using the RAxML 8.1.11 program (Stamatakis et al. 2008). The substitution model applied was the GTRCAT, with a different

Table 1 Taxonomic sampling at genus and species level. Percentage is calculated with respect to number of currently recognized genera and species

Family	Total genera	Included genera		Total species	Included species	
		Number	%		Number	%
Cistugidae	1	1	100.0	2	2	100.0
Craseonycteridae	1	1	100.0	1	1	100.0
Emballonuridae	15	14	93.3	53	39	73.6
Furipteridae	2	1	50.0	2	1	50.0
Hipposideridae	6	4	66.7	81	45	55.6
Megadermatidae	4	2	50.0	5	3	60.0
Miniopteridae	1	1	100.0	25	20	80.0
Molossidae	16	13	81.3	110	51	46.4
Mormoopidae	2	2	100.0	15	10	66.7
Mystacinidae	1	1	100.0	2	1	50.0
Myzopodidae	1	1	100.0	2	2	100.0
Natalidae	3	3	100.0	8	7	87.5
Noctilionidae	1	1	100.0	2	2	100.0
Nycteridae	1	1	100.0	16	7	43.8
Phyllostomidae	59	56	94.9	188	157	83.5
Pteropodidae	45	42	93.3	192	114	59.4
Rhinolophidae	1	1	100.0	83	55	66.3
Rhinonycteridae	4	3	75.0	9	6	66.7
Rhinopomatidae	1	1	100.0	4	3	75.0
Thyropteridae	1	1	100.0	5	3	60.0
Vespertilionidae	54	48	88.9	436	270	61.9
TOTAL	220	198	**90.0**	1241	799	**64.4**

set of parameters for each of seven partitions, which were as follows: the set of coding genes, i.e., the nuclear genes, Cyt-b and ND1, each one divided in first + second positions and third position, and 12S + 16S (i.e., nuclear12, nuclear3, Cytb12, Cytb3, ND112, ND13, and 12S16S). We used the standard hill climbing algorithm (*−f d* option) and 100 replicates to find the best ML tree. Bootstrap values were obtained with 600 replicates (*−b* option) and posteriorly drawn on the

Table 2 Supermatrix details including the markers used, and for each marker, alignment length (bp), number of genera and species included, number and percentage of informative sites, and the percentage of missing data with respect to a total of 824 taxa including outgroups

Marker	Aligned length (bp)	Genera*	Species*	Informative sites		Missing data (%)
				Number	%	
Mitochondrial						
Cyt-*b*	1140	179	695	694	60.88	0.21
ND1	957	70	227	766	80.04	0.73
12S rRNA	728	173	410	383	52.61	0.52
16S rRNA	915	165	397	491	53.66	0.55
Subtotal	**3740**	**187**	**795**	**2334**	**62.41**	**0.49**
Nuclear						
BRCA1	2856	72	93	2832	99.16	0.91
DMP1	1311	68	152	1179	89.93	0.85
RAG1	1038	73	152	721	69.46	0.81
RAG2	1338	169	438	1159	86.62	0.56
vWF	1206	91	136	1166	96.68	0.83
Subtotal	**7749**	**171**	**484**	**7057**	**91.07**	**0.82**
TOTAL	**11,489**	**191**	**799**	**9391**	**81.74**	**0.71**

*excluding outgroups

best tree. These analyses were run on the CIPRES Science Gateway online server (Miller et al. 2010).

Second, we performed a parsimony (MP) analysis using the program TNT 1.1 (Goloboff et al. 2008). Tree search for the total dataset was executed on a cluster of 14 4-core CPUs using a specific script (Appendix 1, Supplementary information) in parallel version of TNT, which applied Sectorial Searches (*Constrained* and *Random* selection for the sectors), Tree Drifting (10 cycles) and Tree Fusing (default options) algorithms implemented in the "Tree Analysis Using New Technologies" package (Goloboff et al. 2003). These search strategies were specifically designed to attack computational problems related to large datasets (Goloboff 1999). All characters were treated as unordered and equally weighted. No constraints were enforced during searches. The strict consensus tree was calculated from the set of most parsimonious trees obtained. Branch stability was estimated with a symmetric resampling (jackknife) analysis based on 500 replicates.

Molecular Dating

We estimated the ages of nodes in the bat phylogeny using fossil calibration and a Bayesian framework with the BEAST 2 software v. 2.3.1 (Bouckaert et al. 2014). First, we reduced the outgroup taxon set to eight terminals to diminish the impact of substitution rate variation across distantly related lineages (Nabholz et al. 2008). Then, we compiled a list of 76 bat fossils primarily from Eiting and Gunnell (2009) and a number of studies, and selected the 44 fossils that could give us approximate minimum ages for corresponding different nodes of the phylogenetic tree obtained in the maximum likelihood analysis (Table 3). These minimum ages were applied as soft-bound priors with log-normal distribution for node ages. The log-normal distribution assigns highest probability for node ages just prior to the fossil age, with a long tail of decreasing probabilities for older ages. For that we selected the clade defined by each calibrated node, set the age of the fossil as the "offset" and selected realistic values for the mean and standard deviation of the log-normal distribution (Table 3). These calibrated nodes were defined as monophyletic. The molecular matrix was partitioned as in the tree searches (see above) and partitions were all analyzed under the GTR + gamma model, with unlinked parameters. The infile was generated with the BEAUTi software (BEAST 2 package) and is available as supplementary data (SI Appendix 2). We did a first run using a random starting tree with 50 million MCMC steps, logging results every 10,000 generations. This run did not reach convergence when checked with Tracer v. 1.6 (Rambaut et al. 2014). We obtained the consensus of the trees generated in this preliminary run and used it as a starting tree in the following runs. Then we rerun the analysis for additional 50 million generations several times, combining the traces (after discarding the first 10% generations as burn in) of each run and rechecking for convergence until it was attained (after five runs). The reason why we did not set a single run with a longer chain length was the computational limit we had with such a large dataset for computation using the CIPRES Science Gateway v. 3.3. Computational limit was also the reason why we kept only 50 trees per run. A larger number of trees would not allow us to use TreeAnnotator (from the BEAST 2 package) to generate a summary dated tree with high posterior density intervals for node ages. The summary tree was then visualized and prepared for publication with FigTree v. 1.4.2 (Rambaut 2014), considering updated taxonomy for taxa entries.

Results and Discussion

Major Phylogenetic Patterns

Our phylogeny included all currently recognized bat families, ca. 90% and 64% of extant diversity at the genus and species level, respectively (i.e., 198 genera and 799 currently recognized species, Table 1). The alignment produced 11,489 nucleotide characters distributed in 3740 bp and 7749 bp of mitochondrial and nuclear sequences, respectively (see Table 2 for supermatrix details and Table SI.2 for accession numbers). Major clades recovered from the various analyses in this study (see below) are summarized in Table 4, and parenthetical trees are shown in SI Appendix 3.

Total Molecular Evidence

The order Chiroptera was recovered as a fully (100%) supported monophyletic group, solidly placed within Laurasiatheria (support >80%), but only weakly joined as sister to the representative of one laurasiatherian group, *Equus* (Perissodactyla; support <50%; Fig. 2). The backbone structure, i.e., those nodes indicating the relationships among major clades within Chiroptera, resulting from both Parsimony analysis (MP) and Maximum Likelihood (ML), is shown in Fig. 3. The ML best tree topology with bootstrap values is shown in Figs. 4, 5 and 6. The strict consensus of the 975 most parsimonious trees, with support values from symmetric resampling indicated above branches, is shown in Figs. SI.14–16. The constituent bat suborders Yinpterochiroptera and Yangochiroptera were recovered as monophyletic with high (e.g., >70%) support (Fig. 3). Within Yinpterochiroptera, two major clades were reconstructed: Pteropodidae and the superfamily Rhinolophoidea, the latter consisting of two groups: (Rhinopomatidae + (Megadermatidae + Craseonycteridae)) and (Rhinonycteridae (Hipposideridae + Rhinolophidae)). Specifically, the genera *Cloeotis* and *Triaenops* (formerly hipposiderids) formed a group, recently recognized at the

Table 3 Extinct taxa used in calibration, and model parameters for Bayesian Analysis (the distributions were all log-normal)

	Extinct taxa	Monophyletic group calibrated by the corresponding extinct taxa	Age (Ma)	Model parameters for Bayesian Analysis				References
				Median	M	S	Offset	
1	*Onychonycteris*	All species	52.5	55.6	6	1	52	Simmons et al. 2008
2	*Saharaderma*	*Craseonycteris, Megaderma, Macroderma*	33.9	36.9	5	1	33.9	Gunnell et al. 2008
3	*Hipposideros*	*Cloeotis, Triaenops, Coelops, Aselliscus, Asellia, Hipposideros, Rhinolophus*	>40	43.6	6	1	40	Eiting and Gunnell 2009
4	*Asellia*	*Asellia, Hipposideros, Coelops, Aselliscus*	>20	24	6	1	20.4	Hand 1997; Eiting and Gunnell 2009
5	*Triaenops*	*Triaenops, Cloeotis*	>5.3	10.9	9	1	5.44	Samonds 2007
6	*Rousettus*	*Rousettus* + endemic African clade	>5.3	10.3	8	1	5.44	Samonds 2007
7	*Tachypteron*	*Nycteris, Saccolaimus, Taphozous, Coleura, Emballonura, Rhynchonycteris, Centronycteris, Saccopteryx, Balantiopteryx, Cyttarops, Diclidurus, Cormura, Peropteryx*	>47	49.4	4	1	47	Storch et al. 2002
8	*Diclidurus*	*Diclidurus, Cyttarops*	>16	19.2	5	1	16.2	Cozzuol 2006
9	*Coleura*	*Coleura, Paraemballonura*	>5.3	9.55	7	1	5.3	Wesselmann 1984
10	*Taphozous*	*Taphozous, Saccolaimus*	>20.4	24.6	7	1	20.4	Butler and Hopwood 1957; Legendre 1980
11	*Peropteryx*	*Cormura, Peropteryx*	>5.3	8.94	6	1	5.3	Czaplewksi and Cartelle 1998
12	*Noctilio*	*Noctilio, Furipterus*	>16	20.2	7	1	16	Czaplewski 1996; Czaplewski et al. 2003b; Cozzuol 2006
13	Undet. Mormoopidae	Phyllostomidae + Mormoopidae	>30	33.6	6	1	30	Morgan and Czaplewski 2012
14	*Mormoops*	*Mormoops, Pteronotus*	>5.3	10.2	8	1	5.3	Silva-Taboada 1974; Morgan and Czaplewski 2003
15	*Desmodus*	*Desmodus, Diaemous*	>5.3	9.55	7	1	5.3	Morgan et al. 1988; Czaplewksi and Cartelle 1998; Czaplewski and Peachey 2003
16	*Micronycteris*	*Lampronycteris, Micronycteris (nicefori), Mimon (bennetti)*	>5.3	10.2	8	1	5.3	Czaplewksi and Cartelle 1998; Czaplewski et al. 2005
17	*Palynephyllum*	Phyllostomidae *(Micronycteris, Lampronycteris, Mimon bennetti, Desmodus, Diaemus, Diphylla, Macrotus)*	>16	20.9	8	1	16	Czaplewski et al. 2003b
18	*Phyllonycteris*	*Erophylla, Phyllonycteris*	>5.3	8.33	5	1	5.3	Silva-Taboada 1974; Morgan and Czaplewski 2003
19	*Leptonycteris*	*Leptonycteris, Glossophaga*	>5.3	8.33	5	1	5.3	Dalquest and Roth 1970
20	*Chrotopterus*	*Vampyrus, Chrotopterus*	>5.3	8.94	6	1	5.3	Czaplewksi and Cartelle 1998
21	*Trachops*	*Macrophyllus, Trachops*	>5.3	8.94	6	1	5.3	Czaplewski et al. 2005
22	*Tonatia*	*Tonatia, Phyllostomus, Phylloderma, Mimon (crenulatum), Lophostoma*	>16	19	5	1	16	Czaplewksi and Cartelle 1998; Cozzuol 2006
23	*Lophostoma, Mimon*	*Phyllostomus (discolor), Phylloderma, Mimon (crenulatum), Lophostoma*	>5.3	9.55	7	1	5.3	Czaplewksi and Cartelle 1998; Czaplewski et al. 2005
24	*Carollia*	*Micronycteris, Glyphonycteris, Carollia*	>5.3	9.55	7	1	5.3	Czaplewksi and Cartelle 1998
25	*Chiroderma*	*Vampyressa, Chiroderma*	>5.3	8.33	5	1	5.3	Czaplewksi and Cartelle 1998
26	*Phyllops*	*Phyllops, Stenoderma*	>5.3	6.51	2	1	5.3	Suárez and Díaz-Franco 2003

Table 3 (continued)

Extinct taxa	Monophyletic group calibrated by the corresponding extinct taxa	Age (Ma)	Model parameters for Bayesian Analysis				References
			Median	M	S	Offset	
27 *Artibeus*	*Dermanura, Artibeus*	>5.3	8.94	6	1	5.3	Dalquest and Roth 1970; Czaplewksi and Cartelle 1998
28 *Natalus*	*Chilonatalus, Natalus*	>5.3	8.94	6	1	5.3	Czaplewksi and Cartelle 1998; Morgan and Czaplewski 2003
29 *Cuvieramops*	Molossidae, Vespertilionidae, Miniopteridae, Cistugidae	>37.2	39.6	4	1	37.2	Legendre 1985; Gunnell and Simmons 2005
30 *Mormopterus*	Molossidae, excluding *Cheiromeles*	>17.5	21.7	7	1	17.5	Czaplewski 2005
31 *Eumops*	*Cynomops, Eumops, Molossops, Nyctinomops*	>16	19	5	1	16	Eiting and Gunnell 2009
32 *Promops*	*Promops, Molossus*	>5.3	8.33	5	1	5.3	Czaplewksi and Cartelle 1998
33 *Khonsunycteris*	Vespertilionidae	>34	36.9	5	0,8	33.9	Gunnell et al. 2008
34 *Kerivoula,*	*Kerivoula, Harpiocephalus, Murina, Harpiola*	>5.3	9.55	7	1	5.3	Horáček 1986; Cermák et al. 2007
35 *Myotis paradaubentonii*	*Myotis daubentonii, M. bechsteini*	>5	7.12	3	1	5.3	Topál 1983; Horáček 2001
36 *Nycticeius*	*Idionycteris, Nycticeius*	>5.3	9.55	7	1	5.3	Butler and Greenwood 1965
37 *Rhogeesa*	*Anthrozous, Rhogeesa* (excluding *R. alleni*)	>16	19.6	6	1	16	Czaplewski et al. 2005
38 *Lasiurus*	*Euderma, Lasiurus*	>11.6	16.5	8	1	11.6	Eiting and Gunnell 2009
39 *Corynorhinus*	*Corynorhinus, Plecotus rafinesqui, Otonycteris*	>11.6	16.5	8	1	11.6	Handley 1959; Topál 1989a, 1989b
40 *Plecotus*	*Plecotus, Barbastella, Corynorhinus, Plecotus rafinesqui, Otonycteris*	>16	21.5	9	1	16	Eiting and Gunnell 2009
41 *Perimyotis*	*Perimyotis, Parastrellus*	>5.3	10.2	8	1	5.3	Ray 1967; Morgan 1991
42 *Lasionycteris*	*Lasionycteris, Hesperonotus, Arielulus, Glauconycteris*	>5.3	11.4	9	1	5.3	Dalquest 1978
43 *Vespertilio*	*Vespertilio, Philetor, Tylonycteris, Hypsugo, Falsistrellus, Vespadelus, Nyctophyllus, Chalinolobus, Nycticeinops, Neoromicia, Laephotis*	>16	18.4	4	1	16	Engesser and Ziegler 1996; Rossina et al. 2006
44 *Submyotodon*	*Submyotodon, Eudiscopus, Myotis*	>11	15.2	7	1	11	Ziegler 2003

family level (Rhinonycteridae; see Foley et al. 2015), sister to a clade containing the hipposiderids sensu stricto plus a monophyletic Rhinolophidae. Craseonycteridae appeared sister to Megadermatidae (ML) or nested within it (MP).

Within Yangochiroptera, three major clades were distinguished: 1) Emballonuroidea with Myzopodidae nested within it (ML and MP: Myzopodidae + Nycteridae formed a group), although the dated tree (BI) showed Myzopodidae sister to Emballonuroidea (see below; Figs. 7, 8 and 9); 2) Noctilionoidea as currently recognized (Fig. 1) except for Myzopodidae, with differences in the MP analysis that included Mystacinidae as sister of Thyropteridae, and Mormoopidae paraphyletic with respect to Phyllostomidae, due to the external position of *Mormoops*; and 3) Vespertilionoidea composed of (Natalidae (Molossidae (Miniopteridae (Cistugidae + Vespertilionidae)))). The relationships among these three major clades varied across analyses. In ML and BI Noctilionoidea formed a group with Emballonuroidea, and this entire clade was sister to Vespertilionoidea. In MP, Noctilionoidea was the basal clade, and Emballonuroidea was sister to Vespertilionoidea. As a global result at the genus level (see details below), we found that, out of 106 polytypic genera included in the total dataset, 87 (82%) were reconstructed as monophyletic in the ML best tree topology, and 82 (77%) in the MP strict consensus (see Table 5).

Mitochondrial versus Nuclear Data Partitions

Both the mitochondrial and nuclear analyses recovered much of the structure present in the global analysis; however, the result from the mitochondrial dataset was slightly more resolved. Higher-level differences between these analyses include: only the mitochondrial analysis recovered Yinpterochiroptera and Rhinolophoidea, while only the nuclear analysis recovered Emballonuroidea (Table 4). In both analyses, Noctilionoidea as defined in Teeling et al. (2005) was not monophyletic given the position of Myzopodidae, which was recovered as sister group of Nycteridae in the mitochondrial analysis, and as part of a polytomy with Emballonuroidea and the remainder of Noctilionoidea in the nuclear analysis.

Individual Genes Analyses

The ribosomal genes 12S and 16S supported the suborder Yinpterochiroptera, while 12S so did for Yangochiroptera. Currently recognized "microbat" superfamilies received various levels of support from phylogenetic variation in the sequences used: Rhinolophoidea was supported by BRCA1, DMP1, and mitochondrial markers; Emballonuroidea only by BRCA1; Noctilionoidea by 12S, Cyt-b, BRCA1, and RAG1; and Vespertilionoidea by 16S and DMP1 (Table 4). At the family level, only traditional Hipposideridae would be paraphyletic due to the inclusion of Rhinolophidae, but the recognition of Rhinonycteridae as in Foley et al. (2015; see below) resolves the paraphyly into three mutually monophyletic, family-level clades (Rhinonycteridae sister to reduced Hipposideridae + Rhinolophidae). This pattern appeared in all individual-gene analyses, thus mimicking the findings in total molecular data analyses.

Individual markers contributed resolution of distinct sectors and levels of the phylogenetic hypothesis. For instance, BRCA1 resolved relationships at the superfamily level, but failed to resolve relationships at lower levels, likely due to the paucity of sequence data within families. This was true for most nuclear markers and that is why results from concatenated sequences greatly improved resolution and support at all levels and sectors.

Systematic Interpretation: Relevance of a Supermatrix Approach to Higher-Level Bat Systematics

Our phylogenetic analysis represented a strong test of the current status of bat systematics, both in terms of its relationships with the rest of mammalian orders and within Chiroptera. This test took the form of unconstrained, deep searches of phylogenetic patterns coded in a supermatrix that is dense in taxonomic coverage. The number and importance of phylogenetic relationships that were recovered and corroborated with this unconstrained analysis were truly remarkable. We interpret and discuss these relationships in the following sections, in the light of the total evidence analyses (see above).

The Position of Bats in the Mammalian Tree

This was not a primary target of our analyses because we included a diverse outgroup set primarily to provide a wide comparative frame for character changes that would eventually affect chiropteran relationships (i.e., for confidently rooting the bat sub-network). Still, we recovered the expected result of Chiroptera nested within Laurasiatheria (Fig. 2; see Murphy et al. 2001; Meredith et al. 2011; O'Leary et al. 2013). Within laurasiatherians, bats were part of a polytomy (MP) or appeared resolved as sister to perissodactyls (ML), the latter being a novel but weakly supported relationship that resembles a proposed clade Pegasoferae (which also included pangolins and carnivorans; see Nishihara et al. 2006).

Interfamilial Relationships

We recovered all family-level bat clades organized in two major groups of bats, Yinpterochiroptera and Yangochiroptera, as in Teeling et al. (2005, 2009), Eick et al. (2005), Tsagkogeorga et al. (2013), and others (cf. Agnarsson et al. 2011; see Fig. 3). Yinpterochiroptera (Fig. 4), or Pteropodiformes sensu Hutcheon and Kirsch (2004), comprised the Old World fruit bats, or megabats, in the single

family Pteropodidae, sister to a Rhinolophoidea composed of its "typical yinochiropteran" (sensu Koopman 1993) "microbat" families, Rhinopomatidae, Craseonycteridae, Megadermatidae, Rhinolophidae, the recently recognized Rhinonycteridae (see Foley et al. 2015), and a restricted Hipposideridae (to the exclusion of Rhinonycteridae, discussed below). The first three rhinolophoid families formed a clade sister to the three families of rhinolophoids sensu stricto (see Discussion below).

Yangochiroptera (Figs. 5 and 6), or Vespertilioniformes sensu Hutcheon and Kirsch (2006), comprised three major "microbat" groups, Emballonuroidea composed by "typical yinochiropteran" bat groups (Nycteridae + Emballonuridae) sensu Koopman (1993), and the yangochiropteran Noctilionoidea and Vespertilionoidea (see details below). Remarkably, in ML and BI we recovered Emballonuroidea + Noctilionoidea, thus confirming (a close version of) this grouping first reported by Meredith et al. (2011) and also more recently by Shi and Rabosky (2015). Within Yangochiroptera, only the position of the Malagasy endemic Myzopodidae diverged from previous studies in a significant way (Figs. 3 and 5). Depending on the analysis, *Myzopoda* unexpectedly joined Nycteridae or Emballonuroidea. The position of extant *Myzopoda*, phylogenetically a branch isolated in an endemic enclave, has been contentious, and varied around a position as sister to Vespertilionoidea (Eick et al. 2005; Miller-Butterworth et al. 2007; Meredith et al. 2011) or basal in the large diversification that occurred across the Southern continents, Noctilionoidea (Teeling et al. 2005; Rojas et al. 2016). In our tree, *Myzopoda* is just 1 or 2 SPR (*subtree-pruning-and-regrafting*) steps from any of the alternative positions, and the branches traversed are not particularly well supported, indicating that noctilionoid or vespertilionoid scenarios are relatively weakly contradicted. However, additional external evidence affords support to a connection between Myzopodidae, Emballonuroidea, and Noctilionoidea. First, emballonuroids and noctilionoids, to the exclusion of *Myzopoda*, were recovered in Meredith et al. (2011), suggesting that the variable position of *Myzopoda* does not alter a previously established relationship of the two superfamilies, as recovered also in our study. Second, Shi and Rabosky (2015) recovered a similar grouping but with *Myzopoda* forced (as part of backbone constraints) as sister of Noctilionoidea. Our unconstrained analysis freely placed *Myzopoda* within the larger clade of Emballonuroidea + Noctilionoidea but as sister of the former, rather than the latter. In addition, Agnarsson et al. (2011) recovered a trace of an emballonuroid connection, with *Myzopoda* sister to *Taphozous* (Emballonuridae; but the clade was disconnected from other emballonuroids and nested within vespertilionoids). Third, Volleth (2013) reported chromosomal evolutionary similarities suggestive of a myzopodid-emballonuroid association, as did Carter et al. (2008) for placentation data. Fourth, new myzopodid fossils (two species of *Phasmatonycteris*) have been recovered from up to 37 my old deposits (early Oligocene) of the Fayum Depression, Egypt (Gunnell et al. 2014). Chromosomal and morphological data, and the presence of a myzopodid lineage of Paleogene age in continental Africa, materialize the possibility of an African link between myzopodids and emballonuroids beyond our tree. More data are required to test the likelihood of this connection; still, we support a novel relationship of Myzopodidae to Emballonuroidea as a third, highly relevant alternative to two other positions suggested in previous studies (sister of Noctilionoidea or Vespertilionoidea), and confirm the recently suggested relationship of Emballonuroidea and Noctilionoidea.

The Timing of Bat Diversification

Our estimation of ages of divergence (Figs. 7, 8 and 9; Fig. SI.17), informed by 44 bat fossil calibration points (Table 3), indicated that extant bats last shared a common ancestor at a point estimate of 62 my (crown age; Table 6). This crown age is similar to that reported by Teeling et al. (2005) and older than that of Shi and Rabosky (2015) at 58 mya (Table 6). Our age estimate is shortly after the K-Pg massive extinction event at 66 mya and coincides with the timing of intraordinal diversification of most placental orders (e.g., Meredith et al. 2011). This result strongly rejects the short fuse model of placental diversification, which proposes that intra-ordinal diversification occurred deep in Cretaceous times, thereby providing support for either of two alternatives, the explosive model and the long fuse model, which share the hypothesis that all intraordinal diversification occurred around the Cretaceous-Paleogene (K-Pg) boundary (see Archibald and Deutschman 2001 for further details on the placental diversification models). The latter two models differ in the timing of inter-ordinal diversification: the explosive model places both the interordinal and intraordinal diversification around the K-Pg boundary (e.g., Gingerich 1977), whereas the long fuse model places the interordinal diversification in the Cretaceous (c. 100 mya in Meredith et al. 2011) and the intra-ordinal diversification right after the K-Pg boundary. Our dataset was not designed to discern between these models at the inter-ordinal level, but the dataset did include a wide sample of outgroups from several placental orders, and so it provided incidental support for the explosive model given that bats last shared a common ancestor with other placental orders only c. 67 mya; i.e., near or around the K-Pg boundary (stem age) as predicted for this model by Archibald and Deutschman (2001).

During this short time distance, the bat lineage evolved powered flight, echolocation, and a myriad of adaptations that affect virtually all organ systems (reviewed in the context of the origin of bat flight in Giannini 2012). By the early Eocene bats had reached a cosmopolitan distribution and soon diversified into many families, nine of which are represented by

Table 4 Major clades recovered from parsimony analysis of individual genes, mitochondrial and nuclear data partitions, and the total dataset, and Maximum Likelihood analysis for the total dataset. Crosses correspond to recovered (monophyletic) groups. Parentheses indicate number of unexpectedly missing (−) and/or extra (+) terminals in a given group. Blank indicates group missing; dash indicates inapplicable cases (lack of sequences for the marker in a given group).

Clade	Individual genes									Mitoch. markers	Nuclear markers	Total dataset (MP)	Total dataset (ML)
	12S	16S	Cyt-*b*	ND1	vWF	BRCA1	RAG1	RAG2	DMP1				
Yinpterochiroptera	X (+1)	X								X		X	X
Pteropodidae	X	X	X	X	X (−2)		X	X (−7)		X	X	X	X
Rhinolophoidea	X	X (−2)	X	X (−1)		X (−1)			X	X		X	X
Hipposideridae					-	-			-	X	X	X (−1)	X
Megadermatidae	X	X	X (+1)	-			X		-	X (+1)	X	X (+1)	X
Rhinolophidae	X	X	X	X	-	-	X	X (−1)	-	X	X	X	X
Rhinonycteridae	-	-		-	-	-	-	-	-	X	-	X	X
Rhinopomatidae	-	-	X	-	-	-	-	-	-	X	-	X	X
Yangochiroptera	X		X							X	X	X	X
Emballonuroidea				-		X (−1)					X	X (+2)*	X (+2)*
Emballonuridae		X	X (−4)	X (−1)	X		-	X (−3)		X	X	X	X
Nycteridae	X	X	X	-	X	X			-	X	X	X	X
Noctilionoidea	X (−1)		X (−3)			X (−4)	X (−4 + 1)			X (−2)	X (−1)	X (−2)*	X (−2)*
Mormoopidae	X			X (−2)		-	-	X (−2)	-	X	X	X (−2)	X
Myzopodidae	-	-	X	-	-	-	-	-	-	X	-	X	X
Noctilionidae	X	X	X	-		X		X	X	X	X	X	X
Phyllostomidae	X (−1)		X (−1)	X (+6–1)	X (+2–2)	X (−2)	X		X	X	X	X	X
Thyropteridae	X	X	-	-	-	-	-	X	X	X	X	X	X
Vespertilionoidea		X (+1–3)							X (−5)	X	X	X	X
Cistugidae	-	-	X	-	-	-	-	-	-	X	-	X	X
Miniopteridae	X	X	X	X (−1)	X		-	X (−1)	X (−1)	X	X	X	X
Molossidae	X	X	X	X	X (−1)				X (+1–1)	X	X	X	X
Natalidae	X	X	X	-	-	-	-	X		X	X	X	X
Vespertilionidae	X (+1)	X (−1)	X (+2)	X (+3)	X		X (−1)			X	X	X	X

Mitoch Mitochondrial

*Two Myzopoda species

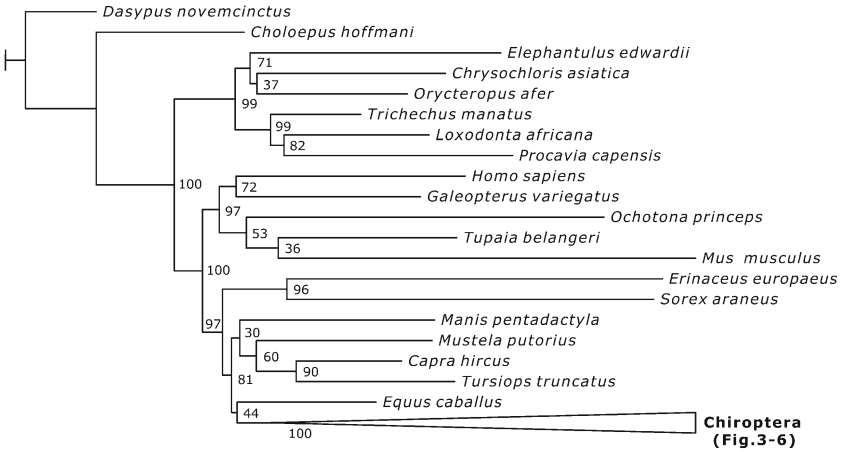

Fig. 2 Position of Chiroptera within Mammalia according to Maximum Likelihood (ML) analysis, showing the supported monophyly of the order and its inclusion in Laurasitheria

fossils (reviewed in Smith et al. 2012). Only one of these nine families survived to the Recent—the extant Emballonuridae. Given the nested position of Emballonuridae in the bat phylogeny, the implication is that many bat families were already in existence by the middle Eocene (Gunnell and Simmons 2005); this attests to the observation that the fossil record of bats is depauperate as compared with other contemporary mammalian clades (Eiting and Gunnell 2009).

Stem and crown age of bat families are presented in Table 6, in which we compared our estimates with those from three previous studies (Teeling et al. 2005; Jones et al. 2005; Shi and Rabosky 2015). Our estimates are more similar to those of Teeling et al. (2005) and Jones et al. (2005), which together tend to be younger (in Vespertilionidae, Molossidae, Natalidae, Phyllostomidae, Mormoopidae, Rhinopomatidae) or much younger (in Noctilionidae, Furipteridae, Craseonycteridae, Megadermatidae) than those of Shi and Rabosky (2015; Table 6). The extreme case is Rhinolophidae, with crown age

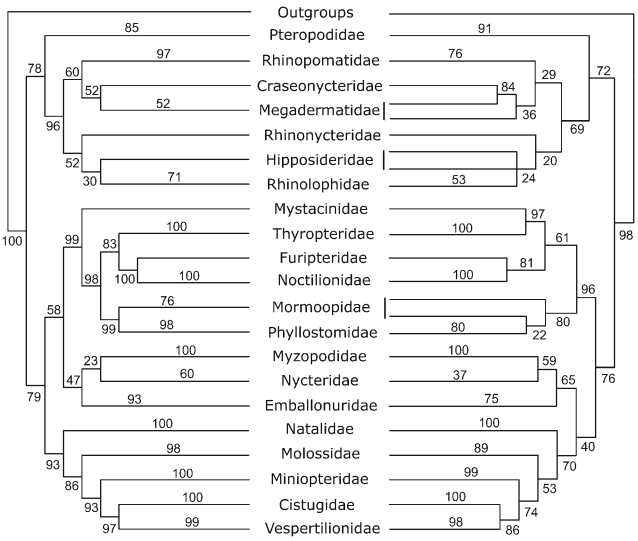

Fig. 3 Systematic interfamilial relationships within Chiroptera, according to Maximum Likelihood (left) and Parsimony (right) criteria. Bootstrap values are indicated

varying from 6.5 my (Jones et al. 2005) to 14.3 my (our study) as compared with minimum 37.2 my in Shi and Rabosky (2015). Other studies afford support to a more recent crown age for rhinolophids, particularly Foley et al. (2015) who dated the family at c. 17 my. Therefore, we believe that the rhinolophid diversification is safely interpreted as a middle Miocene event. Pteropodidae is a similar case; crown age is only 25.9 my in our study (even less in Teeling et al. 2005), and over 40 my in Shi and Rabosky (2015). Other discrepancies included a few older dates as compared with Shi and Rabosky (2015); e.g., Nycteridae is 16 my younger in Shi and Rabosky (2015). Overall, the temporal pattern is one of near K-Pg origination, Paleocene-early Eocene major diversification (period during which 13 extant and eight fossil families appeared), followed by extraordinary crown-group diversification later during the Eocene, with the appearance of additional Neogene crown groups among which we include Natalidae and the speciose Rhinolophidae, Hipposideridae, and Pteropodidae. Recent studies also documented a burst of speciation within genera during the last million year (e.g., in *Pteropus*, Almeida et al. 2014).

The Systematics of Major Bat Groups

Pteropodidae

Megabats compose a rather morphologically and genetically homogeneous, but taxonomically diverse, group of Old World phytophagous bats, including fruit bats and flying foxes specialized in various degrees to feed on fruit and flower products (Kunz and Pierson 1994). Almost nothing of the traditional classification of Andersen (1912), who recognized two major subfamilies on the basis of diet (the nectarivorous Macroglossinae and the frugivorous Pteropinae = Pteropodinae), and a third appended subfamily to contain the aberrant Harpy fruit bats (Harpyionycterinae), was recovered in this study or in any previous phylogenetic analysis. More recently Bergmans (1997) recognized six extant subfamilies (Pteropodinae, Nyctimeninae, Harpyionycterinae, Rousettinae,

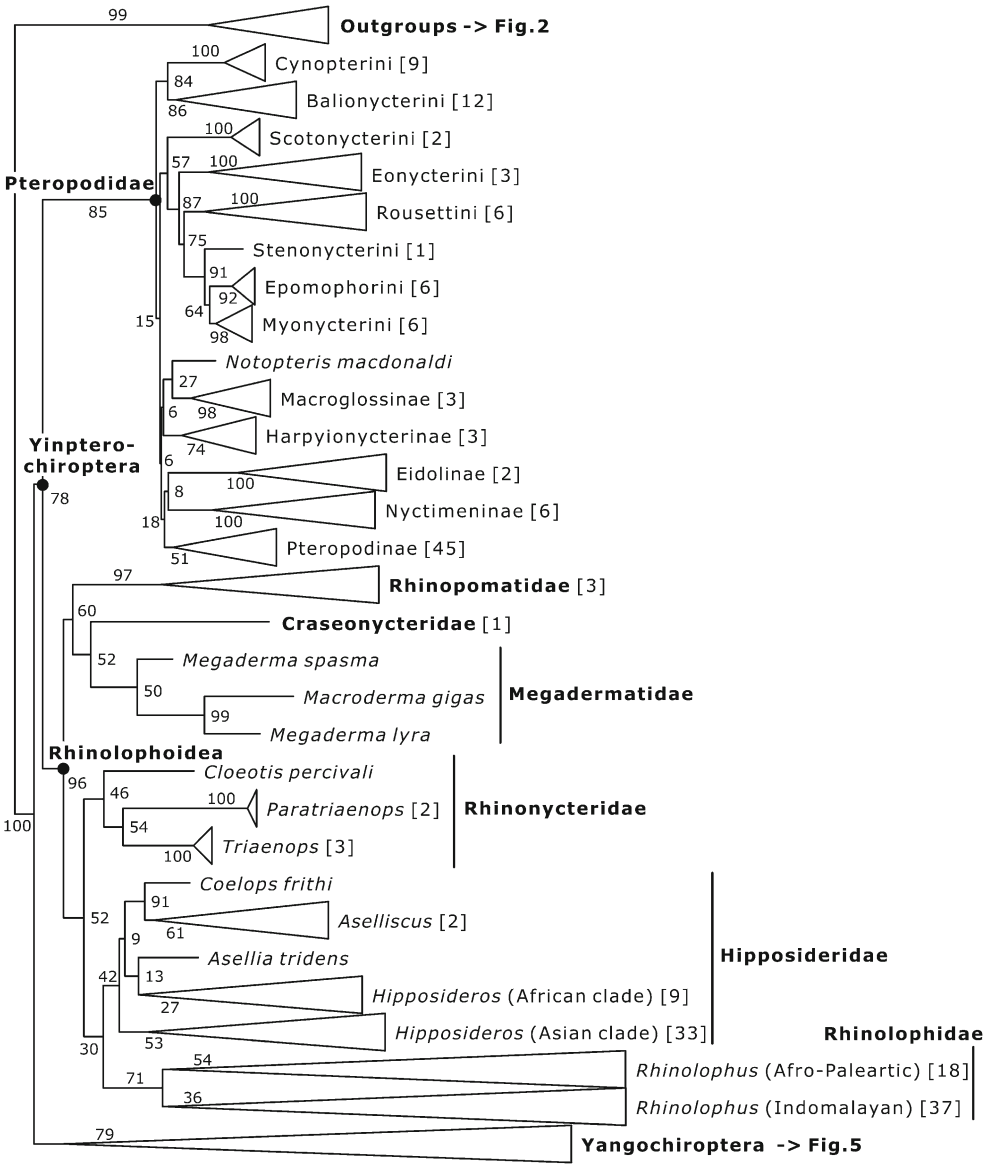

Fig. 4 Maximum Likelihood best tree topology showing systematic relationships within Yinpterochiroptera. Bootstrap values are indicated. The number of terminals considered in our analysis and summarized within each clade is represented by the number between square brackets

Epomophorinae, and Cynopterinae) with numerous tribes, and one additional subfamily Archaeopteropinae to contain the Oligocene fossil from Italy, *Archaeopteropus transiens*, today removed to an *incertae sedis* position (see Schutt and Simmons 1998). Recent studies have confirmed many of Bergmans (1997) groupings (see Giannini and Simmons 2003, 2005) but continued revision has prompted further significant changes. Our results, based on 90% of genera represented, confirmed two trends from most previous studies: the reciprocal monophyly of several, up to seven highly supported subfamilies and their numerous subordinate tribes, united by poorly resolved, never well supported relationships among these subfamilies. The lack of resolution and support in the tree backbone has remained in spite of the permanent accruement of new sequences and terminals that today cover the whole diversity known for the family. This result could not be explained by any detectable systematic bias in the data or incongruence among loci (Almeida et al. 2011). Simulation tests pointed to closely-spaced cladogenesis as the most likely explanation for the poor resolution of the deep pteropodid relationships, and suggested that an increase in the amount of new sequence data (about double than is currently available) is likely to solve this problem (Almeida et al. 2011). Here the backbone problem remained unassailable, because the present study was based on available sequences only. It is clear that the pteropodid backbone requires significant additional effort in the detection of new informative markers and generation of many new sequences. This effort should be circumscribed to increased sampling within pteropodids, considering that the other source of potentially useful information, represented by the contribution of a highly enriched outgroup as in our study, was indecisive to help locate the most likely branch that roots the pteropodid subtree.

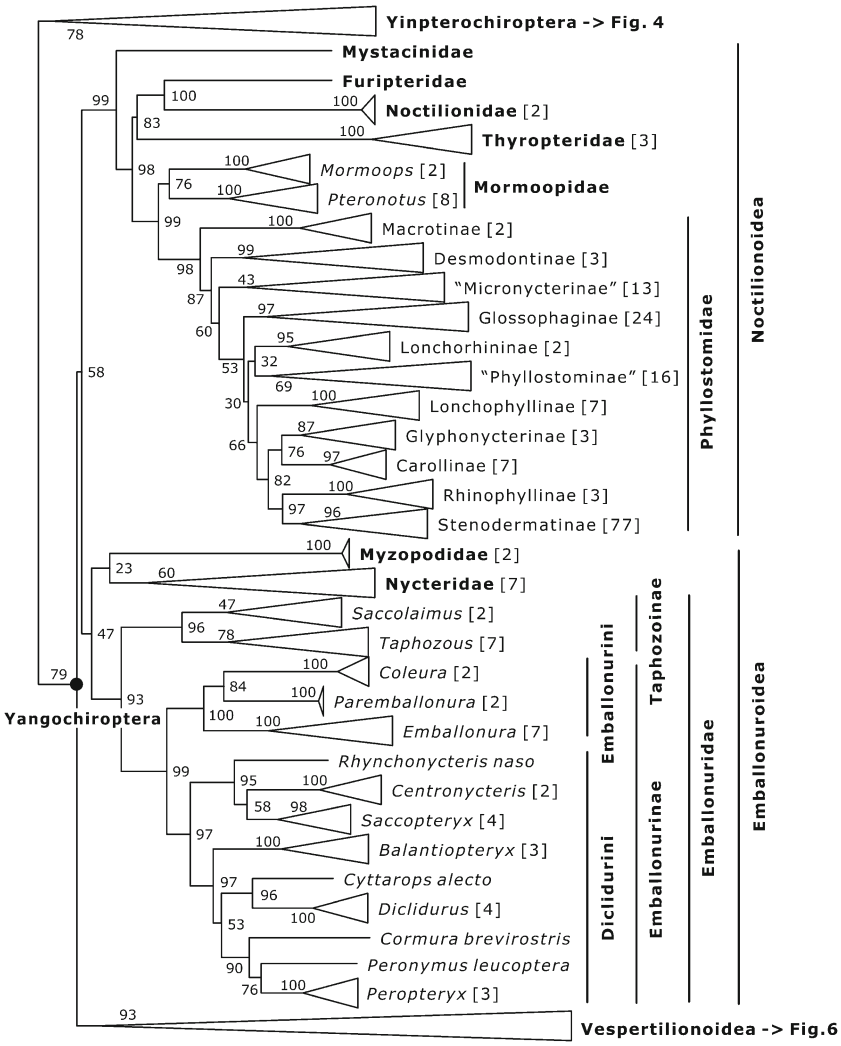

Fig. 5 Maximum Likelihood best tree topology (*cont.*) showing systematic relationships within Yangochiroptera (in part): Noctilionoidea + Emballonuroidea. Bootstrap values are indicated. The number of terminals considered in our analysis and summarized within each clade is represented by the number between square brackets

Our study recovered seven subfamilies (Fig. 4) as in Almeida et al. (2011) but with different successive ordering of branches, difference likely due simply to backbone instability (here Cynopterinae, Rousettinae, Macroglossinae, Harpyionycterinae, Eidolinae, Nyctimeninae, and Pteropodinae). Shi and Rabosky (2015) obtained yet another configuration of groups, with cynopterines and rousettines forming a subclade sister to another subclade grouping the remaining megabat terminals; the internal groupings of pteropodids (discussed below) were similar in Shi and Rabosky (2015) except for the isolated position of *Pteralopex atrata* (a typical pteropodine in our analysis, as expected) and few other details.

The Cynopterinae reflected the division into two tribes, Cynopterini and Balionycterini (Fig. 4), and the internal branching of Almeida et al. (2009), with minor differences in clades of the latter tribe (position of the Indian endemic *Latidens salimali*, relative branching inside the subclade of *Balionycteris*, *Thoopterus*, and *Aethalops*; Fig. SI.1). The next subfamilial clade corresponded to the recent rearrangement of certain traditional rousettine and all epomophorine groups (tribes) proposed by Almeida et al. (2016), who adopted Rousettinae to include Scotonycterini, Eonycterini, Rousettini, Stenonycterini, Myonycterini, and Epomophorini (Plerotini, not included in our study and constituted solely by the Wetter-Zambezian-miombo-woodland endemic *Plerotes anchietae*, which may be sister to either of the latter two tribes; Almeida et al. 2016). The removed position of *Scotonycteris* and *Casinycteris* (Fig. SI.1), as opposed to an expected close affiliation with typical epomophorines (e.g., Bergmans 1997), was previously reported by Almeida et al. (2011, 2016) and Hassanin (2014), Hassanin et al. (2015). Particularly Hassanin et al. (2015) suggested a significant role of Pleistocene refugia and major river barriers of the Central African rainforest blocks in shaping the speciation history of this group. The next four tribes contained species with former rousettine affinities. *Eonycteris*, *Rousettus*, and *Stenonycteris* (formerly subgenus of *Rousettus*) formed successive sister clades of the myonycterines and epomophorines since the first widely comprehensive molecular and morphological studies on megabats

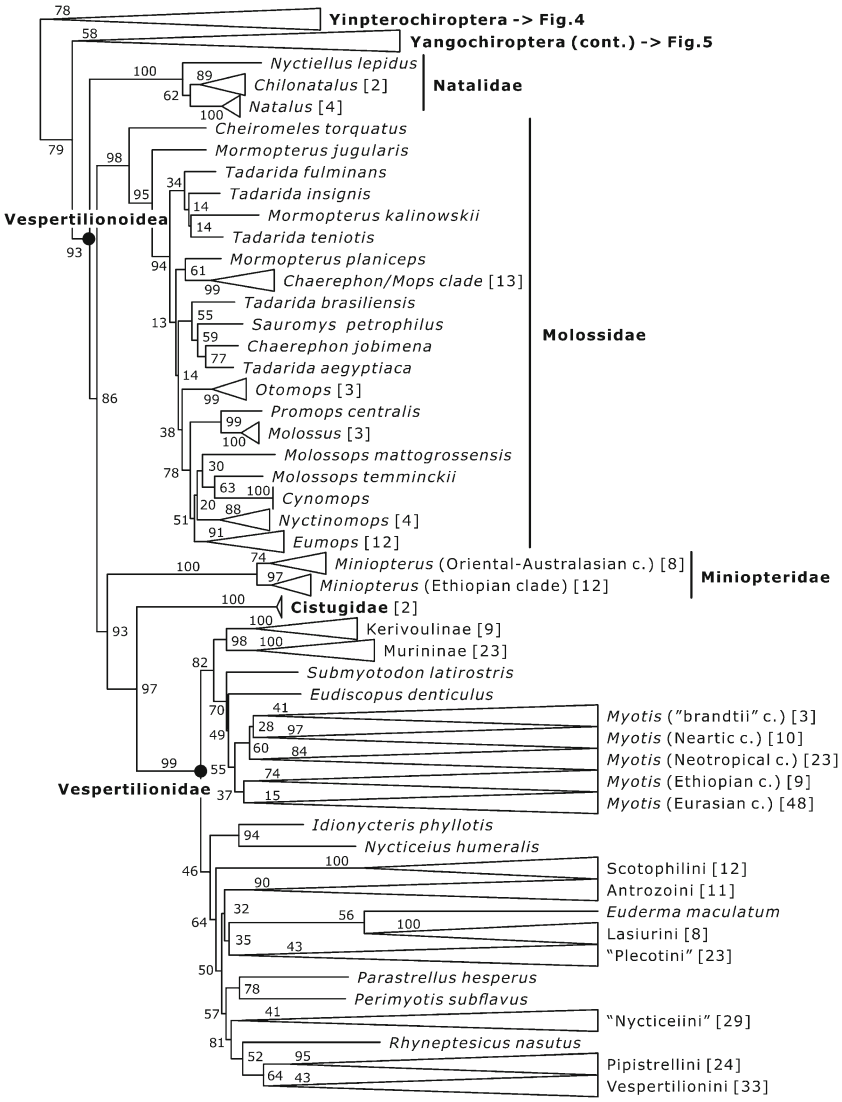

Fig. 6 Maximum Likelihood best tree topology (*cont.*) showing systematic relationships within Yangochiroptera (in part): Vespertilionoidea. Bootstrap values are indicated. The number of terminals considered in our analysis and summarized within each clade is represented by the number between square brackets [Abbreviations: c. clade]

(Giannini and Simmons 2003, 2005), and were consistently recovered in all subsequent studies (Almeida et al. 2011; Nesi et al. 2013; Hassanin 2014). This first led Nesi et al. (2013), and Hassanin (2014) and Almeida et al. (2016), to recognize tribal distinction to all three groups. Relationships within *Rousettus* suggested an ample SE Asian origin of the genus with a single invasion of predominantly African and Indian Ocean species (see Almeida et al. 2016). The current understanding of Myonycterini reflects the discovery of a large endemic African clade composed of members of three apparently disparate traditional subfamilies (the former Macroglossinae, Epomophorinae, and Cynopterinae; see Hollar and Springer 1997). However, detailed analyses lend morphological support to this grouping (Giannini and Simmons 2005) that we recovered here with a similar topology to those of the latest focused analysis of Nesi et al. (2013) and Almeida et al. (2016), with one potentially significant difference, the sister position of *Myonycteris angolensis* (formerly in *Lissonycteris*) to the other congener species (three of four included here; Fig. SI.1). The species missing here (*M. leptodon*) was nested among the other three in Nesi et al. (2013), so *Lissonycteris* may be valid if further support is accrued. The last rousettine clade contained the most typical African megabats, Epomophorini, with genera *Hypsignathus*, *Epomops*, *Nanonycteris*, and species of *Micropteropus* and *Epomophorus*, known to have diverged only very recently and to compose a complex of species of difficult resolution (not addressed here but see Almeida et al. 2016 and citations therein).

The remainder of pteropodid clades contained mainly Australasian taxa with one remarkable exception (the African *Eidolon*, discussed below). Again, none of the basal nodes connecting the subfamilies were supported (Fig. 4; Fig. SI.1); in the first branch off, the Fijian endemic *Notopteris macdonaldi* joined the quintessential Australasian nectarivorous clade, the highly supported Macroglossinae inclusive of *Macroglossus* and *Syconycteris*. The position of *Notopteris* has fluctuated

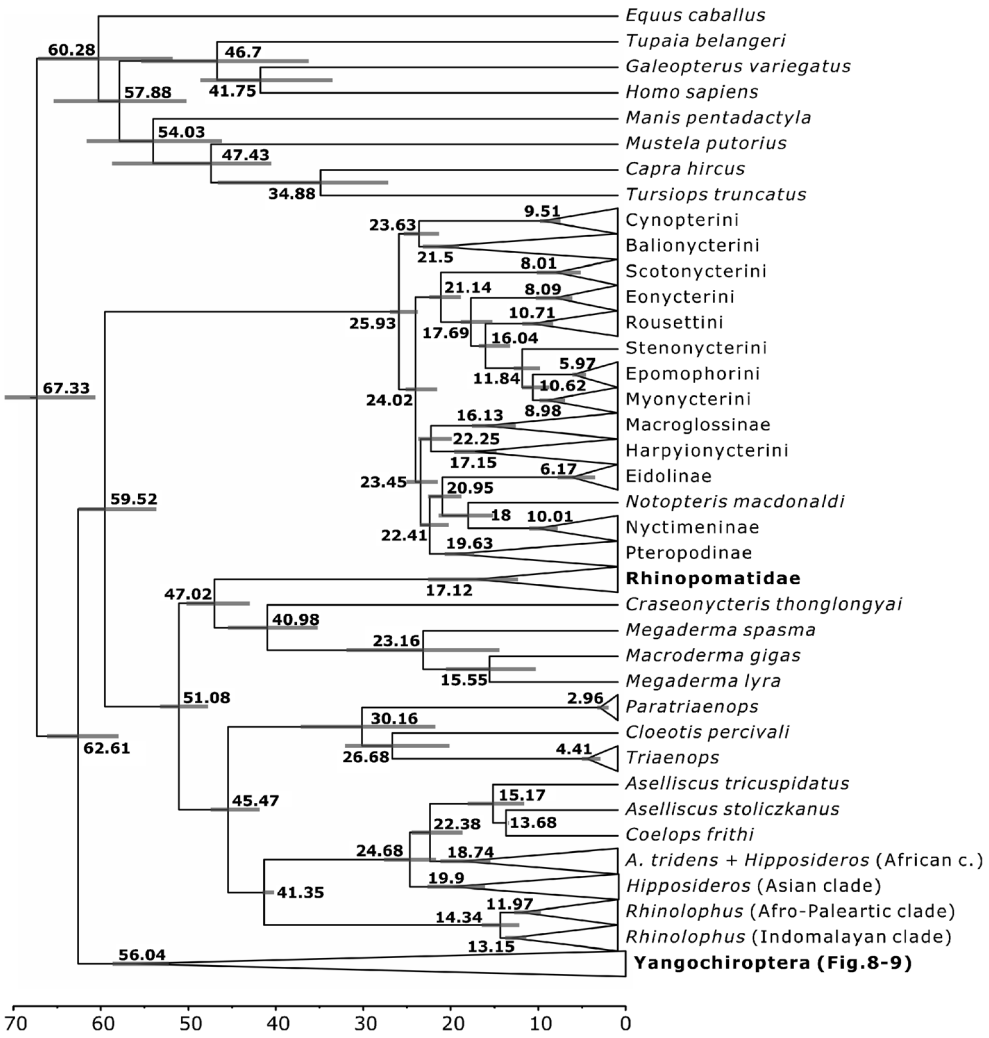

Fig. 7 Molecular dating obtained from a Bayesian analysis, showing Yinpterochiroptera [Abbreviations: A. *Asellia*, c. clade]

considerably across the megabat tree (c.f. Giannini and Simmons 2003, 2005; Almeida et al. 2011); perhaps it is a true macroglossine bat, as historically understood (Andersen 1912) and as suggested here albeit weakly; *N. macdonaldi* is also a specialized nectar feeding bat, as is its sister species (*N. neocaledonica*; not included here, which is another, geographically distant, island endemic). The next clade was the recently reorganized Harpyionycterinae (Fig. 4), originally one of the three megabat families (Andersen 1912) and now known to contain also the Sulawesian endemic *Boneia* (formerly a subgenus of *Rousettus*) and the bare-backed bats (*Dobsonia*; Giannini et al. 2006). The peculiar dentition (with resemblance to a tribosphenic structure) led some old authorities to consider *Harpyionycteris* the basal megabat genus; the deeply nested position recovered by Giannini et al. (2006), and also here, strongly suggests that the dentition is derived and probably associated with a specialized diet (phytophagous durophagy?). The supported, respective monophyly of *Boneia* + *Harpyionycteris* and the bare-backed bats (the New Guinean endemic, first known as subfossil, monotypic *Aproteles*, and the diverse *Dobsonia*) warrants tribal recognition for these two clades.

The next clade, containing the two species of *Eidolon*, is composed of a widespread form *E. helvum* characterized by large, migrating, panmictic populations across the African continent (Juste et al. 1999; Peel et al. 2013), and the Malagasy endemic *E. dupreanum* (Fig. SI.1). *Eidolon* shares morphological characteristics and has been associated with pteropodines (Giannini and Simmons 2005), but posterior studies indicated that this clade represented an isolated African offshoot that has been recently recognized as a separate subfamily (Eidolinae, Almeida et al. 2011, 2016). Nyctimeninae (tube-nosed bats) is a highly supported group that comprises *Nyctimene* and *Paranyctimene* (Simmons 2005) that is in urgent need of systematic revision. Here we included species of *Nyctimene* and recovered the subfamily deeply nested inside the megabat tree (with a near zero support for an association with *Eidolon*; see backbone problem discussion above; Fig. 4). Alternative, more likely positions of tube-nosed bats include near basal (Giannini

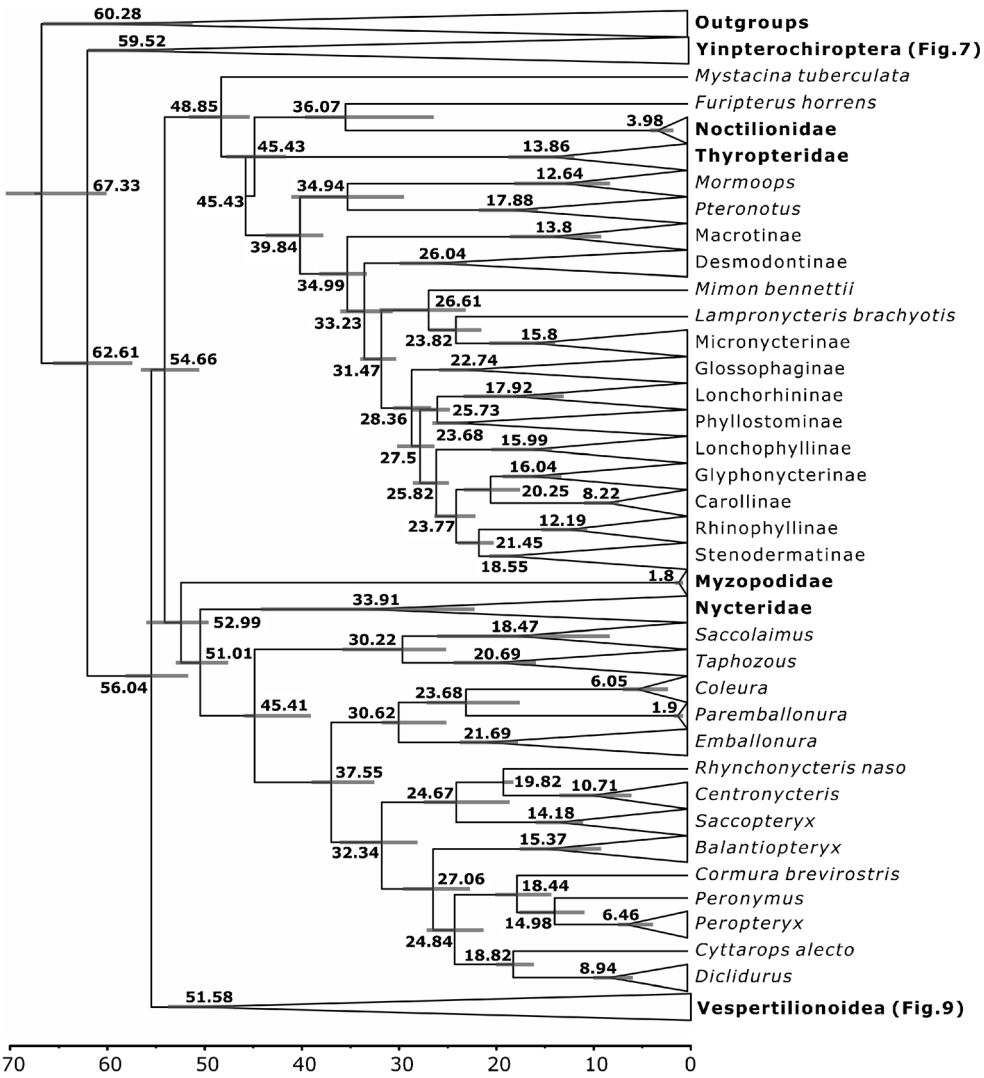

Fig. 8 Molecular dating (*cont.*) obtained from a Bayesian analysis, showing Yangochiroptera (in part): Noctilionoidea + Emballonuroidea

and Simmons 2003) or with a close relationship with cynopterines (Giannini and Simmons 2005) or pteropodines (Almeida et al. 2011).

The last large megabat clade, Pteropodinae, was recovered with moderate to low support (Fig. 4 and Fig. SI.1) but reaffirming its previously recognized composition of E Pacific island endemic monkey faced bats (*Mirimiri* and *Pteralopex*) associated with the Philippine endemic *Desmalopex* (formerly *Pteropus*) in the subgroup (Giannini et al. 2008; Esselstyn et al. 2008); the nectar feeding *Melonycteris* (including the supported recovery of subgenus *Nesonycteris*); the isolated Sulawesian endemic *Styloctenium wallacei* (Philippine endemic *S. mindorensis* not included but see Esselstyn 2007); the close, well-supported association of *Acerodon*; the form *personatus* (probably not a *Pteropus*); and the highly diverse, typical *Pteropus* species forming a clade (see Almeida et al. 2014). The topology within *Pteropus* (Fig. SI.1) reflects that of Almeida et al. (2014), with the *molossinus* group and the isolated *P. scapulatus* as successive sisters of an isolated *P. temminckii* (not a *capistratus* species group member) and the successive species groups *samoensis*, *capistratus*, *vetulus*, *ocularis*, *ornatus*, *griseus*, *poliocephalus*, *livingstonii* and *vampyrus* (new species groups defined by Almeida et al. 2014). This intense, recent (< 1 mya) diversification (Almeida et al. 2014) has been characterized as morphologically plastic, with limited correspondence with morphotypes of former taxonomic utility (e.g., with independent origination of traits associated with nectar feeding habits, or of skull robustness; O'Brien et al. 2009; Almeida et al. 2014). Speciation of this clade is thought of as biogeographically driven, i.e., with groups of species formed in defined geographic regions (O'Brien et al. 2009; Almeida et al. 2014). A prominent example was represented by the recovery here of the clade comprising species of the *livingstonii* group from East African islands that was sister to the *vampyrus* group, with member species primarily distributed in islands and land masses around the Indian Ocean Basin and known to contain species from different four of

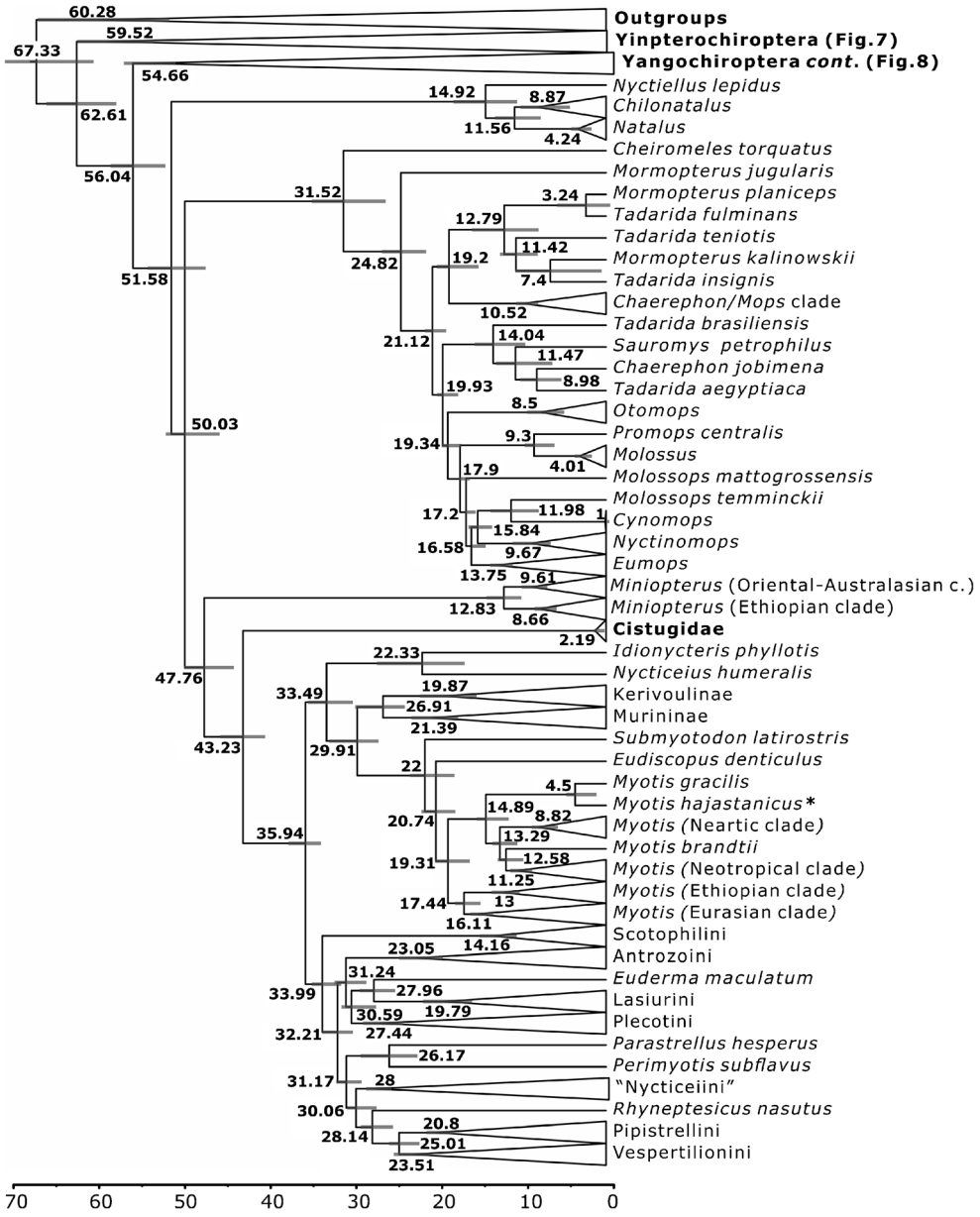

Fig. 9 Molecular dating (*cont.*) obtained from a Bayesian analysis, showing Yangochiroptera (in part): Vespertilionoidea. According to one anonymous reviewer, the terminal *Myotis hajastanicus* (marked *) is represented by an erroneous chimeric combination of *Myotis gracilis* and *Bos javanicus* for cyt-b [Abbreviations: c. clade]

the previously defined, now discarded morphological species groups (see O'Brien et al. 2009; Chan et al. 2011; Almeida et al. 2014).

Rhinolophoidea

Rhinolophoidea was highly supported and divided into two major subclades, one comprising Rhinopomatidae, Craseonycteridae, and Megadermatidae, dated c. 47 mya (Fig. 7; Fig. SI.17), and another subclade inclusive of all members of a traditional Hipposideridae (paraphyletic, see below) and Rhinolophidae (Fig. 4), dated 45 mya (Fig. 7; Fig. SI.17). This arrangement coincided approximately with recently recovered topologies (e.g., Teeling et al. 2005; Meredith et al. 2011; Foley et al. 2015; Shi and Rabosky 2015). In the first subclade, Rhinopomatidae was sister of Craseonycteridae + Megadermatidae as in Teeling et al. (2005; cf. Shi and Rabosky 2015), thereby rejecting initial suggestions of rhinopomatoid (i.e., Rhinopomatidae + Craseonycteridae sensu Simmons and Geisler 1998) affinities of the rare Thailand and Myanmar endemic *Craseonycteris*. Rhinopomatids showed rather ancient crown divergence (up to 17 mya; Table 6), with *Rhinopoma hardwickei* sister to *R. microphyllum* + *R. muscatellum* (Fig. SI.2) as in Hulva et al. (2007), Akmali et al. (2011), and Shi and Rabosky (2015). The Australasian species of megadermatids included *Megaderma spasma* sister to *Megaderma lyra* + *Macroderma gigas* (Fig. 4 and Fig. SI.2). Ours analyses lacked African megadermatids, but Shi and

Table 5 Number of non-monophyletic and monophyletic genera per family recovered in the maximum likelihood best tree and the parsimony strict consensus tree

Family	Total of non-monotypic genera	ML		MP	
		Monophyletic genera	Non-monophyletic genera	Monophyletic genera	Non-monophyletic genera
Cistugidae	1	1	0	1	0
Emballonuridae	10	10	0	8	2
Hipposideridae	2	1	1	1	1
Megadermatidae	1	0	1	0	1
Miniopteridae	1	1	0	1	0
Molossidae	10	5	5	4	6
Mormoopidae	2	2	0	2	0
Myzopodidae	1	1	0	1	0
Natalidae	2	2	0	1	1
Noctilionidae	1	1	0	1	0
Nycteridae	1	1	0	1	0
Phyllostomidae	25	21	4	19	6
Pteropodidae	18	15	3	15	3
Rhinolophidae	1	1	0	1	0
Rhinonycteridae	2	2	0	2	0
Rhinopomatidae	1	1	0	1	0
Thyropteridae	1	1	0	1	0
Vespertilionidae	26	21	5	22	4
TOTAL	106	87	19	82	24

Rabosky (2015) included the East African *Cardioderma cor,* which grouped with the northern Australian *Macroderma*. The paraphyly of *Megaderma* in our study and in Shi and Rabosky (2015) indicates the likely validity of *Lyroderma* Peters, 1872 (currently a subgenus of *Megaderma* containing *M. lyra*).

Hipposiderids, as traditionally recognized, were not monophyletic. Members of the recently recognized Rhinonycteridae (here *Cloeotis* and the *Triaenops* complex included, *Rhinonicteris* absent), formerly a tribe or subfamily of Hipposideridae, were sister to a Hipposideridae restricted to contain the remainder of hipposiderid genera (*Asellia*, *Aselliscus*, *Coelops*, and *Hipposideros*, with the second and last genera paraphyletic), and the monotypic Rhinolophidae (Fig. 4). By contrast, Shi and Rabosky (2015) recovered a monophyletic Hipposideridae with *Rhinonicteris* not associated with *Cloetis* and the *Triaenops* complex, thus rendering Rhinonycteridae paraphyletic. Foley et al. (2015) recovered rhinonycterids as sister to the restricted Hipposideridae and provided molecular and phylogenetic evidence of the distinctiveness of rhinonycterids. *Cloeotis* was sister to the *Triaenops* complex—Tribe Triaenopini —which divided into mutually monophyletic *Triaenops* and *Paratriaenops* (as in Benda and Vallo 2009; cf. Foley et al. 2015).

Hipposideridae sensu Foley et al. (2015) branched off from stem rhinolophids (see below) c. 41 mya (Fig. S17) and divided, some c. 25 mya (Fig. S17), into a subclade of predominantly Asian *Hipposideros* sister to two subclades, *Coelops* + *Aselliscus* on one hand (as in Li et al. 2007 and Tu et al. 2015), and *Asellia* + African *Hipposideros* on the other hand (with the exception of African *H. jonesi* which grouped with the Asian species; Fig. 4). This result is in accordance with the rejection of the monophyly of *Hipposideros*, as traditionally understood, by data from morphology (Sigé 1968; Legendre 1982; Bogdanowicz and Owen 1998) and diverse DNA sequences (e.g., Agnarsson et al. 2011; Foley et al. 2015). In Shi and Rabosky (2015) the African *Hipposideros* were dispersed in three clades among Asian species (*H. commersoni*, *H. cyclops* + *H. gigas*, and the African members of the *bicolor* species group). In addition, the rare *Anthops ornatus* (most likely a species of *Hipposideros*, not included here) grouped with the Asian *Hipposideros* in a previous study (Foley et al. 2015). Our topology included 42 species of *Hipposideros* (Fig. SI.2); if our topology were pruned to contain only the ten species included in Foley et al. (2015), the analyses would differ markedly chiefly because in Foley et al. 2015 the African *H. abae* and *H. caffer* nested within the Asian clade in addition to *H. jonesi*, thus requiring a third independent invasion of Africa by ancestral hipposiderids. The analyses also differed in the rooting of the Asian subclade; re-rooting our topology in the *larvatus-armiger* group as in Foley et al. (2015) would resolve much of the conflict (see also Shi and Rabosky 2015). Simmons (2005; modified from Hill 1963 and Koopman 1994)

Table 6 Comparison of stem/crown ages of Chiroptera and bat families across studies. Ages in million years

Clades	Teeling et al. (2005)	Jones et al. (2005)	Shi and Rabosky (2015)	This study
Chiroptera	NA/64.0		NA/58	67.3/62.6
Cistugidae	NA	NA	NA	43.2/2.2
Craseonycteridae	38.9/38.9	12.0/12.0	51.9/NA	41.0/NA
Emballonuridae	52.1/46.1	53.7/45.0	52.8/47.7	51.0/45.4
Furipteridae	36.2/0.1	50.1/0.1	42.9/NA	36.1/NA
Hipposideridae	NA	NA	NA	51.1/45.5
Hipposideridae **	34.9/34.8	28.7/26.5	49.9/49.3	41.3/24.7
Megadermatidae	38.9/38.9	43.5/39.2	53.4/27.2	41.0/23.2
Miniopteridae	NA	NA	NA	47.8/12.8
Molossidae	49.3/38.2	47.1/35.7	53.8/45.2	50.0/31.5
Mormoopidae	38.8/34.2	37.1/33,7	43.3/39.2	39.8/34.9
Mystacinidae	46.1/46.1	42.8/42.8	50.3/NA	48.8/NA
Myzopodidae	51.6/51.6	51.8/51.8	54.1/1.1	53.0/1.8
Natalidae	51.4/17.3	50.1/15.1	54.8/43.0(22.2)***	51.6/14.9
Noctilionidae	36.2/2.6	42.7/3.0	42.9/13.0	36.1/4.0
Nycteridae	52.1/26.1	43.4/26.2	52.8/17.9	51.0/33.9
Phyllostomidae	38.8/28.1	37.1/27.4	43.3/34.0	39.8/35.0
Pteropodidae	55.8/24.6	61.7/36.1	56.6/40.2	59.5/25.9
Rhinolophidae	34.9/8.7	28.7/6.5	49.9/49.8(37.2)***	41.3/14.3
Rhinonycteridae	NA	NA	NA	45.1/30.2
Rhinopomatidae	39.0/19.4	12.0/9.5	51.9/26.9	47.0/17.1
Thyropteridae	42.1/15.0	50.2/12.9	46.8/13.8	45.4/13.9
Vespertilionidae	NA	NA	NA	43.2/35.9
Vespertilionidae *	49.3/49.2	47.1/47.0	52.1/51.1	50.0/47.8

NA non-applicable, non-available

*Includes Miniopteridae and Cistugidae

**Includes Rhinonycteridae

***Ages varying with assumptions (in parenthesis), see Shi and Rabosky (2015)

provisionally recognized nine species groups in *Hipposideros*, which we refer here below (all represented here with the exception of the Red Sea region, monotypic *megalotis* group). The African *Hipposideros* subclade had the Malagasy *H. commersoni* sister to the other eight species included (note that in the BI tree *Asellia* is sister to *H. commersoni*; Fig. SI.17). Shi and Rabosky (2015) recovered *H. commersoni* in isolation among other hipposiderid genera, whereas the other African *Hipposideros* grouped with the Asian species. The African *Hipposideros* included basal members of the *commersoni* species group (*H. commersoni* and *H. gigas*) and the related *cyclops* species group (represented by *H. cyclops*); and, more derived species in the *speoris* group (*H. abae*) and the large, predominantly Asian *bicolor* group (*H. tephrus*, *H. caffer*, *H. beatus*, *H. ruber*, and *H. fuliginosus*) of which at least the first three species listed belong in the *galeritus* subgroup of Hill (1963). It is clear that these three species groups are not monophyletic and perhaps the most appropriate systematic treatment is the inclusion of all these species in one African species group.

Asian *Hipposideros* were moderately supported and split into several poorly supported subclades that again rendered non-monophyletic all but one of the traditionally recognized species groups. Members of the *bicolor* species group were basal to this subclade and split into a large group (16 species) of *bicolor*-group species, and another group in which three *bicolor*-group species were basal to members of the remainder of species from Asian species groups. In the first group, one subclade was well supported and included the remainder of Hill's (1963) *galeritus* subgroup (here *galeritus*, *cervinus*, *pygmaeus*, and *coxi*), and the other group was essentially a contemporary version of Hill's (1963) *bicolor* subgroup. The topology of this subgroup was congruent with that reported by Guillén-Servent and Francis (2006) with minor differences (position of *H. pomona*); within this subgroup, the relationships of *H. pomona* + (*H. bicolor* + *H. cinerascens*) to other *Hipposideros* were also present in Thong et al. (2012a). As shown by Guillén-Servent and Francis (2006), the morphologically similar *H. ridleyi* did not grouped with those species of the *bicolor* complex, but with *H. ater* instead (and here also

with *H. fulvus*). The latter three species formed a group sister to the other typical *bicolor* subgroup, and New Guinean and Bismarck Is. *H. calcaratus* was sister to all of these species. *Hipposideros obscurus*, *H. speoris*, *H. jonesi*, and *H. coronatus* from the *bicolor* and *speoris* species groups, joined variously across analyses, in all with negligible support, around a well-supported clade of 13 terminals split into two subclades, belonging to four traditional species groups. Of these, only one was recovered here, the *pratti* species group formed by *H. lylei*, *H. scutinares*, and *H. pratti* (see Robinson et al. 2003), which were nested in the first subclade with members of the *armiger* and *diadema* species groups. These species included part of the *H. turpis* complex, dissected by Thong et al. (2012b). We recovered the paraphyletic pattern found by Thong et al. (2012b) by which *turpis* and *alongensis* (including subspp. *Alongensis* and *sungi*) were mixed with species of the *diadema* group (including *diadema*, *lekaguli*, *pelingensis*), whereas the other former member of the complex (*H. pendelburyi*) appeared distantly located within the second subclade among species of the *armiger* (*armiger*, *griffini*) and *larvatus* (*larvatus*) species groups, as in Thong et al. (2012a).

Rhinolophidae, as expected, included only the diverse *Rhinolophus* (>80 currently recognized species) and it was a supported major bat clade that diversified c. 14 mya (Table 6). Csorba et al. (2003) allocated *Rhinolophus* species to 15 species groups (see also Simmons 2005), but it was certain that the phylogenetic structure was more cohesive and that several species groups joined themselves in higher-level clades (see Guillén-Servent et al. 2003). In our analysis, with 55 species included, *Rhinolophus* split into two moderately-to-well-supported groups (Fig. 4), the Afro-Paleartic clade first recognized by Guillén-Servent et al. (2003), and an Indomalayan clade (with a few Australasian species also included), first recovered here. Shi and Rabosky (2015) covered a similar species sample but the Afro-Paleartic *Rhinolophus* were deeply nested among Asian species as in Foley et al. (2015). The Afro-Paleartic clade (Fig. SI.2) included all Sub-Saharian, circum-Mediterranean, and temperate Paleartic forms from six species groups (*landeri*, *capensis*, *maclaudi*, *fumigatus*, *ferrumequinum*, and *euryale*) subsumed in subgenus *Rhinolophus* in Guillén-Servent et al. (2003; see also Zhou et al. 2009). The divergence pattern in this clade is nearly identical to that of Zhou et al. (2009), with two members of the *landeri* species group (*alcyone* and *landeri*) forming a fully (100%) supported clade sister to two well-supported groups, the *capensis* species group (with all its four species represented) and a heterogeneous mixture of the other five species groups. The recently described *R. xinanzhongguoensis* (Zhou et al. 2009) branched first (probably deserving its own species group); this taxon was sister to two groups, one with *R. blasii* (*landeri* species group) and two species of the *euryale* group, and another one with members of the species groups *maclaudi* (monophyletic), *fumigatus*, and *ferrumequinum*.

The Indomalayan Region is the area with the greatest diversity of rhinolophids (Csorba et al. 2003), and here we recovered a well-supported (BS = 84%) clade that included all the Indomalayan forms as well as the few (three out of four species in our analysis) eastern species of Australasian *Rhinolophus* (Fig. SI.2). By contrast, the internal branching of the Indomalayan clade was not well supported; the first split separated members of the *hipposideros* and *trifoliatus* species groups with terminals arranged as in Volleth et al. (2015), versus a larger, more complicated clade with *R. yunanensis* (*pearsoni* species group) sister to a complex of 30 species previously allocated to seven species groups, of which just two (*euryotis* and *rouxii*) were monophyletic. Some of these groupings were monophyletic in previous studies (e.g., the *pearsoni* group in Bailey et al. 2016; see below). However, in our case a few re-arrangements would greatly improve the perceived taxonomic utility of some of these species groups by redefining their membership with minor changes. In one case, only one species of those present (*R. acuminatus*) did not join its group (the *pusillus* group, with the other seven species forming a clade), so the species might be removed to preserve the group. In another case, two groups (the *megaphyllus* and *philippinensis* species groups), here comprising 13 species altogether, were paraphyletic because four species did not group with the other members (*R. affinis*, *R. borneensis*, *R. malayanus*, and *R. stheno*), and because of the inclusion of *R. philippinensis* in the *megaphyllus* species group. However, the core of both groups were sister and so they might be fused to form a single group (here comprising nine species to the exclusion of the outlying species). At least two of the outlying species (*R. affinis* and *R. stheno*) could safely be transferred to the *euryotis* species group.

The arrangement of Indomalayan species of *Rhinolophus* is novel and differs variously from precedent studies. To our knowledge, in no case these species were previously recovered in one group, but the studies further differed in the basal species or group, and in the internal relationships they recover. Focusing on more recent and comprehensive studies, some members of the *trifoliatus* and *hipposideros* groups (subgenera *Aquias* and *Phyllorrhina* in Guillén-Servent et al. 2003; Zhou et al. 2009) were recovered as basal. Stoffberg et al. (2010) recovered a single species (*R. pearsoni* from the small *pearsoni* species group also inclusive of *R. yunanensis*), as sister to all other *Rhinolophus* species; however, no species of the potentially basal *trifoliatus* group was included. Other groupings were remarkably congruent with our results, and this extends to the Afro-Paleartic clade—except that this clade was nested within Indomalayan species and groups in all previous studies. Finally, Bailey et al. (2015) and Foley et al. (2015) used massive and diverse sequence data obtained from very few species selected to represent the most divergent

groups within *Rhinolophus* (seven or eight species groups included out of 15 recognized in Csorba et al. 2003). Their results differed among themselves and with respect to our study, in several ways. Most remarkably, differences were in the nested relationships of representatives of the Afro-Paleartic clade with respect to the Indomalayan species (basal next to the *trifoliatus* group in Bailey et al. 2016, or sister to the *hipposideros* group in Foley et al. 2015), and in the recovery of the basal most species or clade—a member of the *trifoliatus* group (*R. formosae*) in Bailey et al. (2015) or a clade composed of members of three species groups (*euryale*, *ferrumequinum*, and *hipposideros*) in Foley et al. (2015). To conclude, the phylogeny of *Rhinolophus* continues in a state of flux given the disparity of results from different studies; our study in particular contributed one of the largest terminals set to date (55 species) and recovered groups with a strong geographic imprint, principally revealed in the Afro-Paleartic versus Indomalayan major clades.

Emballonuroidea

Formerly inclusive also of other yinochiropteran families, this superfamily is now reduced to Nycteridae and Emballonuridae (see Simmons and Geisler 1998 for review). In all our analyses, the Myzopodidae appeared related to emballonuroids (see discussion above). In this section we focus on nycterids and emballonurids and their internal phylogenetic relationships (Fig. 5).

No molecular phylogeny of the monotypic Nycteridae was available until recently (see Shi and Rabosky 2015). Stem nycterids are reconstructed to split from emballonurids at an age as old as 51 mya (Fig. 8; Fig. SI.17) and to begin modern diversification some 33 mya (Table 6). The morphological phylogenies (Griffiths 1994, 1997) agreed only limitedly with Shi and Rabosy (2015) and with our nycterid subtree (Fig. SI.3). The African *Nycteris macrotis* was sister to a clade containing the two Asian species, and another clade with the remainder of African species included. This nested Asian clade is the only one exactly represented in morphological phylogenies (cf. Griffiths 1997). In Shi and Rabosky (2015) the groupings were markedly different, but the nycterid history remains essentially the same: one of a Paleogene lineage of rather homogeneous African species, several with ample distribution in the continent, with a single dispersion to Asia and limited spread in the new continent (both Asian species, *N. tragata* and *N. javanica*, are restricted to islands of the Sundaland region). A still missing part of this history is represented by the Malagasy endemic *N. madagascariensis*, neither included here nor in Shi and Rabosky (2015).

Emballonuridae represents an ancient lineage, here dated 51 my (stem) and 45 my (crown; Table 6; Fig. 8), and represents the single extant family so far identified to be already present by the middle Eocene amidst a constellation of fossil bat families (see Smith et al. 2012). Besides adding species to previous phylogenies, our topology composed an interesting combination of previous molecular studies in a single subtree (Fig. 5 and Fig. SI.3). Taphozoinae was sister to Emballonurinae, which in turn was divided into Emballonurini and Diclidurini; all this major clades were highly supported, and they reflected the hypotheses already advanced by Robbins and Sarich (1988) and Griffiths and Smith (1991). In our phylogeny, a single New World clade (Diclidurini), dated 32 my (crown age; Fig. 8; Fig. SI.17), was nested among Paleotropical clades. Also fossils, particularly *Tachypteron franzeni* from the early middle Eocene of Grube Messel, Germany (Storch et al. 2002), attests an Old World origin of emballonurids. Relationships within Taphozoinae included the monophyly of both member genera, *Saccolaimus* (two species included, paraphyletic in Shi and Rabosky 2015) and *Taphozous* (six species included, paraphyletic in Shi and Rabosky 2015). In *Taphozous*, a monophyletic Australian clade nested among successive branches of predominantly SE Asian species (plus one distributed in scattered spots from W Africa to India, *T. nudiventris*). However, this view should be taken with caution given that other African, Afro-Malagasy, Asian, and Australian species exist but were not included in this study. Emballonurini replicated the pattern of Afro-Malagasy genera (*Coleura* + *Paremballonura*) versus Indo-Pacific *Emballonura* recovered originally by Goodman et al. (2012) and Ruedi et al. (2012), and also Shi and Rabosky (2015). The position of the controversial Wallacean-Papuan *Mosia nigrescens* was not addressed in this study (see Lim et al. 2008; Colgan and Soheili 2008); Shi and Rabosky (2015) recovered *Mosia* nested among Neotropical forms.

Diclidurini replicated the major branching pattern of, and resolved relationships pending in, the previous most comprehensive analysis of Lim et al. (2008). Here two highly supported groups were recovered, one inclusive of *Rhynchonycteris* and the clade *Centronycteris* + *Saccopteryx*, and one inclusive of the remaining New World genera. In the latter, *Balantiopteryx* was sister to two clades, *Cyttarops* + *Diclidurus* (ghost bats), and the clade (*Cormura* (*Peronymus* (*Peropteryx* spp.))). *Peronymus* is usually treated as subgenus or synonym of *Peropteryx* (e.g., Simmons 2005), but here it was recovered as sister of other three *Peropteryx* species included, suggesting the validity of the genus. This pattern of relationships was also recovered by Shi and Rabosky (2015; saving that *Mosia* was also included in the group). This analysis then resolved the polytomy in the base of Diclidurini in Lim et al. (2008), which is seen to be resolved by defining a sister relationship of *Balantiopteryx* to the other diclidurines (here with only moderate support).

Noctilionoidea

The New Zealand endemic *Mystacina* was sister to the New World diversification of noctilionoids, dated 45 my (stem; Fig. 8; Fig. SI.17). Subsequent groups include one with the small families Thyropteridae, Furipteridae, and Noctilionidae (two to five species each), and another group with Mormoopidae and the speciose Phyllostomidae (Fig. 5). This branching pattern has been recovered for instance in Teeling et al. (2005) and Shi and Rabosky (2015), and differed in the position of Thyropteridae with respect to Eick et al. (2005; sister to *Mystacina*), Meredith et al. (2011), and Rojas et al. (2016; sister to the other New World families).

Thyropteridae is a rainforest clade with diversity peaking in western Amazonia (see Velazco et al. 2014). Our molecular topology (Fig. SI.3) is identical to that of Shi and Rabosky (2015) and Rojas et al. (2016), and compatible with the morphological topology reported by Gregorin et al. (2006), which included one new species (*T. devivoi*). Specifically, *T. discifera* sister to *T. tricolor* + *T. lavali* (with *T. devivoi* sister to *T. lavali* in Gregorin et al. 2006). Affinities of an additional, new species of *Thyroptera* (*T. wynnae* Velazco et al. 2014), which lacked DNA sequences and was not included in any previous phylogeny, remain uncertain. The single furipterid included, *Furipterus horrens* (the other species, the South American West coast desert endemic *Amorphochilus schnabli* lacked DNA sequences as of March 2015; see Materials and Methods), was sister to the monotypic Noctilionidae, with both species of fisherman bats included (*N. albiventris* and *N. leporinus*; Fig. SI.3), as in Shi and Rabosky (2015) and Rojas et al. (2016). Continental wide, high genetic diversity in *Noctilio* has been reported and suggested a recent derivation of the fishing habit in *N. leporinus* (Lewis-Oritt et al. 2001).

The relationship of Mormoopidae and Phyllostomidae, as well as their mutual monophyly, was strongly supported in ML and BI (Mormoopidae paraphyletic in MP) and in most studies, except Agnarsson et al. (2011; Mormoopidae paraphyletic). In the former family, *Mormoops* (two species included) was sister to *Pteronotus* (eight species included; Fig. SI.3). These relationships replicated those reported by Van Den Bussche and Weyandt (2003), Dávalos (2006), and Rojas et al. (2016), with the *Pteronotus parnellii* species complex, subgenus *Phyllodia* (here *P. rubiginosus*, *P. parnellii*, and *P. pusillus*) recovered as sister of the remaining species (note that the situation in *Phyllodia* is more complicated due to additional cryptic species; see Thoisy et al. 2014). In turn, in the sister group *P. personatus* related to the usual species pairs *P. gymnonotus* + *P. davyi* (subgenus *Pteronotus*) and *P. quadridens* + *P. macleayi* (subgenus *Chilonycteris* to the exclusion of *P. personatus*). This scheme is identical to that of Shi and Rabosky (2015) and remarkably similar to the first, morphological phylogenetic hypothesis of Smith (1972) except for the position of *P. personatus* (sister to the *davyi* + *gymnonotus* clade in Smith 1972), and differed from the morphological phylogeny of Simmons and Conway (2001) in the nested position of *P. parnellii* complex and *P. personatus*. The present scheme implies complicated biogeographic processes involving the South American, Central American and Caribbean taxa (see Dávalos 2006).

Recovered here with nearly full support (BS = 98%), Phyllostomidae, here dated 35 my (crown; Fig. 8; Table 6) is arguably one of the largest and functionally most complex diversification of mammals (Dumont et al. 2011). We simplify the systematic analysis with respect to myriad of previous phylogenetic hypotheses by comparing our results primarily with the most recent and comprehensive study of Rojas et al. (2016); we turn to previous, or more group-specific, hypotheses whenever appropriate (see below). The ordering of major phyllostomid subclades in our study was: Macrotinae, Desmodontinae, Micronycterinae, Glossophaginae, Phyllostominae + Lonchorhininae, Lonchophyllinae, Glyphonycterinae + Carollinae, and Rhinophyllinae + Stenodermatinae (Fig. 5). This ordering differed from Rojas et al. (2016) and Shi and Rabosky (2015) in the position of Desmodontinae versus Micronycterinae, Phyllostominae versus Glossophaginae, and Lonchorhininae. Desmodontinae, and Micronycterinae were recovered in the reverse order (Micronycterinae more basal) in Rojas et al. (2016) and most significant previous studies (e.g., Baker et al. 2003, 2012; Datzman et al. 2010; Dumont et al. 2011). The clade Phyllostominae + Lonchorhininae was one node more basal with respect to Glossophaginae in Baker et al. (2012), or just Phyllostominae in Rojas et al. (2016). Our recovery of a sister relationship of Phyllostominae + Lonchorhininae recomposed a traditional subclade of derived phyllostomines (i.e., to the exclusion of *Macrotus* and *Micronycteris*), albeit with poor support. Next we comparatively interpret the relationships within each phyllostomid subclade (Fig. SI.4).

As originally suggested by chromosomal data (see Patton and Baker 1978), the monotypic Macrotinae was recovered with high support (BS = 87%) as sister to all other groups of phyllostomids (Karyovarians sensu Baker et al. 2003). In Desmodontinae, *Diphylla* was sister to *Diaemus* + *Desmodus* as in all recent studies, both morphological (Wetterer et al. 2000) and DNA-based studies (Baker et al. 2003, 2012; Rojas et al. 2016). Relationships within Micronycterinae included *Mimon bennettii* sister to *Lampronycteris* and *Micronycteris* (BA) or *Mimon* + *Lampronycteris* sister to *Micronycteris* (ML, MP). *Mimon* (including *M. bennettii* and *M. cozumelae*) was recovered within Phyllostominae in Rojas et al. (2016; see below). We recovered two groups within a monophyletic *Micronycteris*, both compatible (as groups) with those obtained by Baker et al. (2012) and Rojas et al. (2016) but with minor internal differences within one group. Specifically, one internally fully compatible group composed of *M. yatesi*,

M. minuta, *M. homezi*, and *M. schmidtorum*, and a sister group composed of the successive branches of *M. hirsuta*, *M. brosseti*, and the remaining five species, the latter with different branching pattern as compared with Rojas et al. (2016).

Glossophaginae, its two constituent major subclades, and most internal groupings (recognized tribes and subtribes) were solidly supported and all identical to Rojas et al. (2016) with one minor exception (paraphyly of *Choeroniscus* in our study). As suggested by the branching pattern of the two major subclades, and their high degree of support, the best taxonomic arrangement seems to accept Choeronycterini and its two subtribes (Anourina and Choeronycterina), and recognize the tribe Glossophagini inclusive of subtribes Glossophagina, Phyllonycterina, and Brachyphyllina (Glossophagini, Phyllonycterini, and Brachyphyllini, respectively, in Baker et al. 2003). In our study, Anourina included just two out of no less than ten predominantly, but not exclusively Andean genus *Anoura* of specialized nectarivores (four species included in Rojas et al. 2016). In Choeronycterina, *Hylonycteris* (and *Lichonycteris* in Rojas et al. 2016; not included here) was sister to *Choeroniscus minor* and a clade inclusive of *Musonycteris*, *Choeroniscus goodmani*, and *Choeronycteris* (*Choeroniscus* monophyletic in Rojas et al. 2016). Glossophagina reproduced the branching pattern of previous studies (Baker et al. 2012; Rojas et al. 2016) with the successive sisters *Monophyllus* (Antillean), *Leptonycteris* (Central and Northern South American), and *Glossophaga* (with *G. soricina* widely distributed in the Neotropics and other species more restricted to Central and northern South America).

Support for the relationship Phyllostominae + Lonchorhininae was poor (BS = 32%), in contrast with the high (69–95%) support for each subfamily. Membership of Phyllostominae, as redefined by Baker et al. (2003), was recovered intact in our study, with the exception of *Mimon* (see above). Here the large, carnivorous bats *Chrotopterus* and *Vampyrum* formed the clade Vampyrini (Wetterer et al. 2000; Baker et al. 2003, 2012) sister to Macrophyllini + Phyllostomini (*Mimon* included in the latter in Baker et al. 2003, 2012; Rojas et al. 2016). This clade included members of *Gardnerycteris*, now comprising *crenulatum* (included here) and *koepckeae* (both species formerly in *Mimon*; see Hurtado-Miranda and Pacheco-Torres 2014), *Tonatia*, *Lophostoma*, *Phylloderma*, and a paraphyletic *Phyllostomus* due to the position of *P. discolor* (with *Tonatia* here and in Shi and Rabosky 2015); *Phyllostomus* is (most likely correctly) monophyletic in Rojas et al. (2016). We included two species of *Lonchorhina* (Lonchorhininae), which formed a highly supported (BS = 95%) clade.

The major (unranked) clade Dulcivarians sensu Baker et al. (2003) was moderately supported and included Lonchophyllinae, Carollinae, Glyphonycterinae, Rhynophyllinae, and Stenoderminae. Lonchophyllinae received full support (BS = 100%) and in this group *Hsunycteris* (recently removed from *Lonchophylla*; see Parlos et al. 2014) was sister to a paraphyletic *Lonchophylla* plus the Amazonian *Lionycteris* and the Peruvian desert endemic *Platalina*. Here and in Shi and Rabosky (2015), the paraphyly of *Lonchophylla* was due to the association of *L. mordax* with *Lionycteris* + *Platalina*; in Rojas et al. (2016) paraphyly affects *L. mordax* but in association with *Hsunycteris*; also *L. dekeyseri* and *L. hesperia* (not included here) nested within a clade with *Lionycteris* and *Platalina*. Therefore a full taxonomic revision of *Lonchophylla* is in order.

The clade Nullicauda (as modified by Baker et al. 2003) received high support and included Carollinae, Glyphonycterinae, and the (unranked) Carpovarians (see below). The clade Carollinae + Glyphonycterinae, first recovered by Baker et al. (2003), was relatively well supported. The former sorted *Carollia* species into the usual two groupings, the small *C. castanea* + *C. benkeithi* versus a clade with all other species (arranged as in Velazco 2013). In Glyphonycterinae, *Trinycteris* was sister to *Glyphonycteris* (two species; see Baker et al. 2003).

Carpovarians sensu Baker et al. (2003) comprised Rhinophyllinae + Stenodermatinae. Rhinophyllinae (traditionally associated with *Carollia*) included only *Rhinophylla* with three currently recognized species, with *R. alethina* sister to other two species as in Baker et al. (2012; *R. fischerae* basal in Rojas et al. 2016, but with negligible support).

Stenodermatinae is the largest diversification of phyllostomids, which was associated with the evolution of predominant frugivory and cranial adaptations to this diet (Dumont et al. 2011). The monotypic Sturnirini was highly supported as a group and as sister to the remaining genera, grouped in Stenodermatini (see Wetterer et al. 2000; Baker et al. 2003, 2012; Rojas et al. 2016). *Sturnira bidens* and *S. nana*, both formerly in paraphyletic subgenus *Corvira* (see Velazco and Patterson 2013) were successive sisters to two supported subclades. Subclade A as in Velazco and Patterson (2013) comprised mainly Andean montane rain- and cloud-forest species (eight included here) and the *lilium* group (subclade B in Velazco and Patterson 2013) comprised continental and Caribbean, mainly lowland rainforest species (six included here). Unlike Velazco and Patterson (2013), Rojas et al. (2016), and Shi and Rabosky (2015), *S. aratathomasi* was sister to just one of these groups (subclade B) instead of sister to both subclades together (A + B). In spite of this difference, the pattern of relationships recovered here confirmed the suggestion of an Andean origin for *Sturnira* (see Velazco and Patterson 2013).

Monophyly of Stenodermatini was never seriously challenged; for this group, solid morphological support exists (see Wetterer et al. 2000), as well as support from many independent molecular markers (e.g., Baker et al. 2003, 2012; Dumont et al. 2011; Rojas et al. 2016). The single difference

in suprageneric relationships with all previous studies was the sister relationship between *Enchistenes* and *Ectophylla* (instead of successive sisters of Artibeina + Stenodermatina sensu Baker et al. 2003, as in Shi and Rabosky 2015). Two subclades were recovered, Vampyressina sister of the unranked Mesostenodermatini sensu Baker et al. (2003), the latter comprising *Ectophylla* + *Enchistenes* (each in its own subtribe in Baker et al. 2003), sister of short faced bats Stenodermatina and fruit-eating bats Artibeina. Here Caribbean *Ariteus* + *Ardops* and *Phyllops* + *Stenoderma* were sister to continental short-faced bats (*Centurio*, *Sphaeronycteris*, *Ametrida*, and *Pygoderma*) chiefly as in Baker et al. (2012), whereas continental and Caribbean forms were mutually monophyletic in Rojas et al. (2016). In Artibeina, mutual monophyly and high support (BS > 92%) warranted recognition of three genera, the monotypic *Koopmania*, large fruit-eating bats *Artibeus*, and small fruit-eating bats *Dermanura*, instead of just *Artibeus* as in Van Den Bussche et al. (1998), Wetterer et al. (2000), and most subsequent authors including Rojas et al. (2016). Large *Artibeus* (ten species included) were sister to *Koopmania concolor* (weakly supported sister of *Dermanura* in Redondo et al. 2008), and both grouped with *Dermanura* (11 species included). Relationships within *Artibeus* differed in details from both Lim et al. (2004) and Rojas et al. (2016), but concurred with Rojas et al. (2016) and Larsen et al. (2007) in recovering a subclade of three species (*A. fraterculus*, *A. inopinatus*, and *A. hirsutus*) as sister of the other species (*A. fimbriatus* sister of this group + the remaining species in Lim et al. 2004), which were nearly identical (and fully compatible) to those reported by Redondo et al. (2008). Relationships within *Dermanura* differed from Rojas et al. (2016) in the ordering of species groups; we recovered the subclade of *D. rosenbergi*, *D. azteca*, and *D. watsoni* as sister to other species, as in Redondo et al. (2008; this subclade nested in Rojas et al. 2016, and *D. azteca* nested in Solari et al. 2009). Other subclades were recovered much as in Redondo et al. (2008) and also Solari et al. (2009; except for *D. azteca* and *D. cinerea*), but in different ordering in Rojas et al. 2016. Vampyressina received almost full support but divided into two poorly supported subclades, one inclusive of *Uroderma*, which was sister to the remaining Vampyressina in Rojas et al. (2016) and Shi and Rabosky (2015). In one subclade, *Mesophylla* + *Vampyressa* were sister to *Vampyrodes* and the diverse *Platyrrhinus*. Groupings within the latter nearly replicated the morphological result of Velazco (2005) except for the position of *P. brachycephalus*, here sister to all other *Platyrrhinus* but sister to the *helleri* group in Velazco (2005) and Rojas et al. (2016). In the other subclade *Uroderma* was sister to *Vampyriscus* + *Chiroderma* as in Baker et al. (2012) and Rojas et al. (2016), but in these previous studies *Mesophylla* + *Vampyressa* were sister of this second subclade instead of to the first subclade as recovered here. However these differences involve traversing relatively poorly supported clades both in our study and in Rojas et al. (2016).

Finally, in a recent contribution Baker et al. (2016) proposed a Linnean classification of Phyllostomidae, recognizing 11 subfamilies (Macrotinae, Micronycterinae, Desmodontinae,

Phyllostominae, Glossophaginae, Lonchorhininae, Lonchophyllinae, Glyphonycterinae, Carollinae, Rhinophyllinae, and Stenodermatinae), 12 tribes (Diphyllini, Desmodontini, Macrophyllini, Phyllostomini, Vampyrini, Glossophagnini, Brachyphyllini, Choeronycterini, Lonchophyllini, Hsunycterini, Sturnirini, and Stenodermatini), and nine subtribes (Brachyphyllina, Phyllonycterina, Anourina, Choeronycterina, Vampyressina, Enchisthenina, Ectophyllina, Artibeina, and Stenodermatina). This classification (which naturally did not include the unranked groups mentioned above) was based on the molecular phylogenetic studies cited above, the results of which were highly congruent with ours. All subfamilies, tribes, and subtribes proposed by Baker et al. (2016) corresponded to clades in our phylogeny, with nearly identical membership. The single exception was *Mimon bennettii*, here sister to Micronycterinae but proposed as a member of Vampyrini instead by Baker et al. 2016. Morphological diagnoses for all these clades were provided by Cirranello et al. (2016).

Vespertilionoidea

We recovered the current topology of this superfamily (see Lack et al. 2010; Rohers et al. 2010), dated 51 my (stem; Fig. 9; Fig. SI.17), in all analyses, i.e., the successively nested families Natalidae, Molossidae, Miniopteridae, Cistugidae, and Vespertilionidae (Fig. 6; see also Shi and Rabosky 2015). Natalidae, dated only c. 15 my (crown age; Table 6; Fig. 9) included all three genera and seven out of eight currently recognized species (Table 1). The two polytypic genera (*Natalus* and *Chilonatalus*) were monophyletic and sister to the basal *Nyctiellus*, as in Dávalos (2005). Within *Natalus* two groups were recovered (Fig. SI.3); one group included two distinct Greater Antillean species (*N. jamaicensis* + *N. major*; see Tejedor et al. 2005), and another group included continental and Lesser Antillean species (*N. stramineus* + *N. tumidirostris*).

Molossidae was represented by 51 currently recognized species, i.e., ca. 47% of the extant diversity, and by 13 out of 16 genera (Table 1). This family was particularly problematic given the low support of some key clades and the limited correspondence between these results as well as all previous phylogenetic studies with the current taxonomy (e.g., Simmons 2005). The Sundaic hairless bat *Cheiromeles torquatus* was sister to all other molossids (Fig. 6), confirming previous analyses (Ammerman et al. 2012, 2013). *Mormopterus jugularis* from Madagascar branched after

Cheiromeles; note that the former appeared deeply nested in the phylogeny, as sister to the Neotropical clade, in Shi and Rabosky (2015). The latter study found that the Mauritian *Mormopterus acetabulosus* (not included here) was sister to all molossids instead of *Cheiromeles* (paraphyletic in Shi and Rabosky 2015). With the Peruvian endemic *Tomopeas ravus*, the blunt-eared bat (not included in this study nor in any phylogeny), eventually confirmed as sister to all other molossid bats (see Sudman et al. 1994; Velazco et al. 2013; Gregorin and Cirranello 2015), a relictual, scattered pattern of basal pantropical divergence emerges as characteristic of the family, clearly older that our current crown-age estimation at 31 my (Table 6). After *Cheiromeles*, a paraphyletic array of wrinkle-faced species of *Mormopterus*, *Mops*, *Chaerephon*, *Sauromys*, and *Tadarida* (all genera previously included in *Tadarida*; Simmons 2005) subsequently branched off (Fig. 6). The species *jugularis*, recovered here and in Lamb et al. (2011) as basal (after *Cheiromeles*), is the type of *Mormopterus* and, given its isolated basal position, is clearly the only form that should be included in this genus. This argument is valid also if considering the more nested position of *M. jugularis* in Shi and Rabosky (2015). Next was a poorly supported clade of Old World *Tadarida* species plus the Peruvian endemic "*Mormopterus*" *kalinowski*. This group contained *teniotis*, the type of *Tadarida*. "*Mormopterus*" *planiceps* was sister to a highly supported clade that included an admixture of the majority of our sample of *Mops* and *Chaerephon* (Fig. 6 and Fig. SI.3), strongly suggesting that these genera are synonyms, as suggested by Lamb et al. (2011) pending confirmation from more samples (provided here; *Mops* Lesson, 1842 may have priority over *Chaerephon* Dobson, 1874). Next, another *Tadarida*-like clade was recovered, including members of *Tadarida* (*brasiliensis* and *aegyptiaca*), *Sauromys* and the Malagasy *Chaerephon jobimena* (Fig. 6); Lamb et al. 2011 noted the strong link between *T. aegyptiaca* and *C. jobimena*, also present here. Interestingly, the species *brasiliensis*, type of *Rhizomops*, was sister to the other (African) terminals, so probably this generic name should be applied to species of this (poorly supported) clade or at least to *brasiliensis*. A highly supported *Otomops*, the African mastiff bats (see also Lamb et al. 2011), was sister to the New World clade of molossids (Fig. 6; with "*Tadarida*" (*Rhizomops*) *brasiliensis* as the sole exception). In this clade, the durophagous *Promops* and *Molossus*, characterized by deep, short skulls and vaulted palates, were the first to branch off. In Shi and Rabosky (2015), *Molossus ater* grouped among the basal Paleotropical molossids. The form *mattogrosensis* was sister to small *Molossops* and *Cynomops*, suggesting that *Neoplatymops* Peterson, 1965, is valid and contains the former species (see also Shi and Rabosky 2015). *Nyctinomops* was well supported and represents the native Neotropical group of the wrinkle-faced bats originally included in *Tadarida* (Simmons 2005); our MP analysis recovered the same topology reported in Dolman and Ammerman (2015). *Eumops* represents the largest molossid diversification in the Neotropics (see Medina et al. 2014); 12 out of 16 currently recognized species were included in our analyses. Our tree (Fig. SI.3) and Shi and Rabosky's (2015) grouped some species pairs as in the morphological phylogeny of Gregorin (2009; e.g., *E. dabbenei* + *E. underwoodi*, *E. auripendulus* + *E. maurus*), but the overall relationships were different. By contrast, these relationships were largely congruent with those recovered by Medina et al. (2014), the same as in the ND1 analysis of Bartlett et al. (2013), and differed from their combined analyses only in that *E. hansae* was basal instead of sister to *E. nanus* + *E. patagonicus*. The largest species (e.g., *E. perotis*, *E. dabbenei*) did not group together, which suggests that evolution of size as a key character was considerably complex in *Eumops*.

The monotypic Miniopteridae, here dated just 13 my (stem age; Fig. 9; Fig. SI.17) but estimated to split from other vespertilionoids c. 48 mya (crown age; Table 6; Fig. 9), was recognized as a distinct family with respect to Vespertilionidae only recently (Miller-Buttlerworth et al. 2007). We included 20 of the 24 currently recognized species (Table 1) and they grouped, as first reported by Appleton et al. (2004) and Miller-Butterworth et al. (2005), in two distinct clades that exhibited a strong biogeographical pattern (Fig. 6): 1. an Oriental-Australasian clade, and 2. an Ethiopian clade with a nested Indian Ocean (predominantly Malagasy but also Comoran) clade (see also Juste et al. 2007). The type *M. schreibersii*, was sister to the first major clade (Fig. SI.3). Once thought to be one of the most widespread bat species, subsequently restricted to a wide circum-Mediterranean distribution (Europe, northern Africa and the Near East; see Hutson et al. 2008), the *schreibersii* complex has been further decomposed in more regional cryptic species (see Furman et al. 2010; Bilgin et al. 2012), thus accentuating the hierarchical geographic pattern of speciation in this group (Appleton et al. 2004).

Formerly considered a Myotinae genus, and even a subgenus of *Myotis*, the southern African *Cistugo* was the sole member of the new family erected by Lack et al. (2010) on the basis of profound genetic divergences with respect to vespertilionids. Here, Cistugidae with its two constituent spcies (*C. seabrai* and *C. lesueuri*) was fully supported as a lineage separated from all taxa currently allocated to Vespertilionidae (Fig. 6; see also Shi and Rabosky 2015) since the early middle Eocene (crown age 43 my; Table 6).

In our analysis, the highly supported Vespertilionidae sensu stricto, dated 35 my (crown age; Table 6; Fig. 9; Fig. SI.17) included 270 out of more than 400 described extant species, belonging to 48 of 54 currently recognized genera (Table 1). The main internal structure of the family appeared solidly supported except for Vespertilioninae (Fig. 6); the rapid diversification suggested by Lack and Van Den Bussche (2010) as a

major impediment to the resolution of phylogenetic relationships within the family thus appeared restricted to this poorly supported clade. By comparison, the sister group of Vespertilioninae was a highly supported (unnamed) clade that grouped Myotinae and a clade containing Kerivoulinae and Murininae (all highly supported; Fig. 6). In Kerivoulinae, the type *K. pellucida* was sister to all other species, which grouped in highly supported clades (Fig. SI.5). In Murininae, the speciose *Murina*, one of the bat groups with more recently described (many cryptic) species (e.g., Csorba and Bates 2005; Kruskop and Eger 2008; Furey et al. 2009; Kuo et al. 2009; Csorba et al. 2011; Ruedi et al. 2012; Soisook et al. 2013; Son et al. 2015), has been recovered as paraphyletic in previous studies due the inclusion of both *Harpiocephalus* and *Harpiola* (e.g., Son et al. 2015). In our ML tree, the two species of *Harpiocephalus* formed a clade sister to a *Murina* inclusive of *Harpiola* (Fig. SI.5); in MP, *Murina* was monophyletic (Fig. SI.11), as in Shi and Rabosky (2015). Groupings of *Murina* species were grossly congruent with previous analysis in supported clades (see Ruedi et al. 2012; Son et al. 2015).

Myotinae, dated 22 my (crown age; Fig. 9; Fig. SI.17) included primarily *Myotis* but also *Submyotodon* and the monotypic *Eudiscopus* (Fig. 6). *Submyotodon* was first described as a Middle Miocene (Upper Astaracian, c. 11 mya) fossil from Bavarian karstic fissure fillings (Ziegler 2003). Ruedi et al. (2015) assigned the former *Myotis latirostris*, a Taiwan endemic originally associated with the *muricola* group (see Simmons 2005), to *Submyotodon*, which was recovered here and previously (Ruedi et al. 2013, 2015) as sister to all other myotines. The monotypic *Eudiscopus* occupied the next myotine branch after *Submyotodon*. *Eudiscopus denticulus* was previously included in Vespertilionini (see Simmons 2005) but recovered as sister to a handful of other *Myotis* species included by Borisenko et al. (2008) in their description of a new *Myotis* species (*M. phanluongi*, also included here). Our ML and BI trees support the inclusion of this restricted SE Asian, highly specialized bat in a basal position in the Myotinae. By contrast, the MP analysis placed *Eudiscopus* outside Myotinae (Fig. SI.11 and SI.16), as in Shi and Rabosky (2015); however, Shi and Rabosky (2015) inforced the monophyly of traditional Myotinae (i.e., to the exclusion of *Eudiscopus*). *Myotis* sensu stricto (excluding *latirostris*) was monophyletic. The striking geographic pattern of predominantly New World vs. Old World clades discovered in previous phylogenies of the genus (e.g., Stadelmann et al. 2007; Ruedi et al. 2013, 2015) was replicated here (Fig. 6), although with only moderate support. The New World clade split into the Neotropical subclade, which contained only one unexpected group (the Neartic *M. thysanodes* + *M. lucifugus*, Fig. SI.5) with respect to previous phylogenies (including Shi and Rabosky 2015), and the Neartic subclade; the Paleartic "*brandtii* lineage" (not recovered in Shi and Rabosky 2015) was sister to the Neartic subclade instead of sister to the Neotropical subclade as in Ruedi et al. (2013). In the Old World clade, subclades were recovered in very similar, but not identical, order and composition as in Ruedi et al. (2013; Fig. SI.5); specifically subclades V (in the provisional terminology of Ruedi et al. 2013) with a majority of Ethiopian species but also one Mediterranean and two Asian species (subgenus *Chrysopteron*; see Csorba et al. 2014); subclade VI of "whiskered" *Myotis*; subclade VIII; subclade IV or Oriental subclade sister to *M. muricola* (not grouped with *M. ater* and so subclade VII missing); subclade IX or Asian subclade; subclade X or "trawling" *Myotis*; subclade III including *M. bechsteinii*, *M. daubentonii*, *M. frater*, and *M. sicarius*; and finally subclade II of "large" *Myotis*. "Floating" species in the later study (i.e., *M. alcathoe*, *M. dasycmene*, *M. annectans*, *M. capaccinii*) appeared in quite similar positions in our ML tree, suggesting less ambiguity or conflict in spite of the persistent low support of their position.

Vespertilioninae was poorly supported (Fig. 6; see Lack and Van Den Bussche 2010). Unexpectedly, the North American *Idionycteris* (a plecotine) and *Nycticeius* formed the first branch, with high (94%) support. Bats formerly included in Nycticeiini neither grouped together in the specific work of Rohers et al. (2011) nor here. *Idionycteris* grouped with the North American *Euderma* among other plecotine bats in Shi and Rabosky (2015), and with *Otonycteris* in Roehrs et al. (2011). The next vespertilionine clade was that of a strongly supported Scotophilini, the Old World yellow bats *Scotophilus* (Fig. SI.6); *S. kuhlii* and *S. nux* were successive sisters to ten other species that grouped in a way compatible with previous phylogenies (e.g., Hoofer and Van Den Bussche 2003). The next split divided the subfamily into two poorly supported clades (Fig. 6). One of them included the tribes Antrozoini + (Lasiurini + Plecotini). Antrozoini (Fig. SI.6) was highly supported, with *Baeodon allenni* (formerly *Rhogeessa alleni*) as sister to *Antrozous* + *Bauerus*, and *Rhogeessa* to the exclusion of *alleni* (as in Hoofer and Van Den Bussche 2003). The spotted bat *Euderma maculatum* appeared as sister of lasiurines instead of sister to plecotines as would have been expected, but the very low support of this association suggests that more data would easily favor the alternative, morphologically sensible grouping with plecotines as in Shi and Rabosky (2015). A monophyletic, formerly monotypic Lasiurini (Fig. SI.6) supported the recent generic splits of Baird et al. (2015) into yellow, hoary and red bats, so that *Dasypterus* (here including *ega* and *xanthinus*) was sister to *Aeorestes* (not subgenus of *Myotis*, here including *cinereus*) and *Lasiurus*, with *intermedius* placed here as sister to red bats (as in Shi and Rabosky 2015, but with yellow bats in Baird et al. 2015). Plecotini (Fig. SI.6) included the remainder of large eared bats dealt with so far: i.e., the Neartic *Corynorhinus*, the Paleartic *Barbastella* and *Plecotus*, and the

controversial desert (Saharian through NW Indian) bat *Otonycteris* (see discussion of various proposed affinities of *Otonycteris* in Hoofer and Van Den Bussche 2001, 2003). Shi and Rabosky (2015) also included in this group the New World pipistrelles or perimyotines (*Parastrellus* + *Perimyotis*). In the second large clade, the perimyotines were confirmed here as a group once again (Fig. 6; see Hoofer and Van Den Bussche 2003; Roehrs et al. 2010) and represented the farthest removed lineage from traditional *Pipistrellus*. Next, the last two major groups of vespertilionine bats branched off. The first one included most bats in Nycticeiini sensu Hoofer and Van Den Bussche (2003; i.e., *Lasionycteris*, *Glauconycteris*, *Scotomanes*, *Eptesicus*) plus the pipistrelles in *Arielulus*, the false serotine bat *Hesperoptenus*, and the carnivorous great evening bat *Ia io* (sister to *Scotomanes* as in Thabah et al. 2007 and Shi and Rabosky 2015). The later clade was sister to *Eptesicus*, whose phylogenetic structure was similar to that of Hoofer and Van Den Bussche (2003) and Roehrs et al. (2010) except that *E. fuscus* was sister to Neotropical *Eptesicus* inclusive of big-eared brown bats (subgenus *Histiotus*). Old World *Eptesicus*, subgenus *Cnephaeus* following Hoofer and Van Den Bussche (2003), grouped in much the same way as in Juste et al. (2013), with *E. isabellinus*, *E. hottentotus*, and *E. anatolicus* (not member of the *bottae* complex) as successive sisters to a *bottae* group (to the exclusion of *anatolicus*) and a *serotinus* group. This group as a whole represented approximately the admixture of Nycticeiini and Eptesicini reported in Rohers et al. (2010); if the removal of *Nycticeius* from this group (sister to *Idionycteris*, see above) is confirmed by more data, a possible name for this clade is Eptesicini. Removed from this clade appeared the Sind bat, formerly in *Eptesicus* and now *Rhyneptesicus nasutus* (see Horáček et al. 2000), sister to the true pipistrelles, Pipistrellini (highly supported), and the true vesper bats, Vespertilionini (Fig. 6; poorly supported in ML with 43% bootstrap, well supported in MP with 80% jackknife). Pipistrelles (Fig. SI.6) included *Scotoecus* sister to a paraphyletic array of *Pipistrellus* that included the closely related *Glischropus* (see Csorba et al. 2011, 2015), many typical *Pipistrellus* species, and a nested *Nyctalus* (see Hoofer and Van Den Bussche 2003). Vesper bats (Fig. SI.6) included *Vespertilio*, *Philetor* + *Tylonycteris*, *Falsistrellus* + *Hypsugo* (part), *Vespadelus* + (*Nyctophilus* + *Chalinolobus*), a fully supported *Nycticeinops* + "*Hypsugo*" *eisentrauti*, a *Neoromicia* complex that included another "*Hypsugo*" (*anchietae*), and a monophyletic subclade *Laephotis*. The polyphyly of *Hypsugo* (and *Pipistrellus*) may be fixed by transferring the problematic species to the sister or the more inclusive genera (e.g., as proposed for *Eptesicus*; see Hoofer and Van Den Bussche 2003). These groupings also reflect the necessary breakup in several genera of the former *Pipistrellus* (*Parastrellus*, *Arielulus*, *Falsistrellus*, *Hypsugo*, *Neoromicia*) and *Eptesicus* (*Vespadelus*, *Rhyneptesicus*).

Concluding Remarks

The present study reveals the strength of current bat systematics as tested by machine-intensive, unconstrained phylogenetic analyses of a comprehensive dataset both in terms of taxonomic and character sampling, with updated taxonomy and no chimeric terminals. With this analysis, bats are independently confirmed as a lineage of laurasiatherians that diversified shortly after the K-Pg boundary to immediately split into two large extant clades, Yinpterochiroptera and Yangochiroptera, together comprising 21 recognizable, supported familiy-level clades, with most subdivisions in subfamilies, genera and species groups recovered in much the way as in contemporary studies restricted to each tree sector or level. Here all these systematic hypotheses were tested simultaneously, with more data and without preconceived groupings. The few sectors of the tree requiring full revision / reanalysis are Molossidae, Vespertilioninae, *Hipposideros*, species groups in *Rhinolophus*, and the backbone in Pteropodidae. Running unconstrained analyses also furnish the opportunity for new findings arising solely from data interactions. Here myzopodids constitute an example, as this clade was recovered in a novel position that invited a new interpretation of its relationships and biogoegraphy in the light of shared phenomic characters and the geographic distribution of fossils. Another remarkable result was the monophyly of many complex groups such as Myotinae (constrained in Shi and Rabosy 2015) and *Myotis*, with most of previously reported subclades also recovered in this study (see Ruedi et al. 2013). One emerging pattern of this analysis is the strong geographic imprint on phylogenetic patterns, first seen in several subclades in previous specific studies (e.g., Appleton et al. 2004; Goodman et al. 2012; Ruedi et al. 2013), and here confirmed simultaneously at most levels and sectors in the entire bat phylogeny. To our knowledge, previously unreported relationships that we present as new examples of clearly biogeographic influence on phylogenetic patterns include paraphyly of *Hipposideros* with two separated geographic subclades of African versus predominantly Asian species; and the Indomalayan group in *Rhinolophus*, sister to the Afro-Paleartic clade. The timing of chiropteran diversification, inferred with the control of as many as 44 fossil calibration points in this study, suggested successive diversification events starting early in the Paleocene and continuing throughout the Paleogene and Neogene with the origination of different groups in different continents, up until a burst of species diversification in the last million years in several groups. We conclude that bat systematics is really mature thanks to the dedicated work of many research teams worldwide, with their hypotheses demonstrably capable of passing the rigourous test of large scale, unconstrained analyses only possible with high quality sequence data and intensive analytical tools. We have shown reliable phylogenetic results from these analyses, so

more significant findings await the inclusion of even more species and data.

Acknowledgements We thank the support from Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina, grant PICT 2008–1798 to NPG, and grants PICT 1930_2011 and PIP 0260 to SAC.

References

Agnarsson I, Zambrana-Torrelio CM, Flores-Saldana NP, May-Collado LJ (2011) A time-calibrated species-level phylogeny of bats (Chiroptera, Mammalia). PLoS Curr. doi:10.1371/currents.RRN1212

Akmali V, Farazmand A, Darvish J, Sharifi M (2011) Phylogeography and taxonomic status of the greater mouse-tailed bat *Rhinopoma microphyllum* (Chiroptera: Rhinopomatidae) in Iran. Acta Chiropt 13(2): 279–290

Almeida FC, Giannini NP, DeSalle R, Simmons NB (2009) The phylogenetic relationships of cynopterine fruit bats (Chiroptera: Pteropodidae: Cynopterinae). Mol Phylogenet Evol 53(3): 772–783

Almeida FC, Giannini NP, DeSalle R, Simmons NB (2011) Evolutionary relationships of the Old World fruit bats (Chiroptera, Pteropodidae): another star phylogeny? BMC Evol Biol 11(1): 281

Almeida FC, Giannini NP, Simmons NB (2016) The evolutionary history of the African fruit bats (Chiroptera: Pteropodidae). Acta Chiropt 18: 73–90

Almeida FC, Giannini NP, Simmons NB, Helgen KM (2014) Each flying fox on its own branch: a phylogenetic tree for *Pteropus* and related genera (Chiroptera: Pteropodidae). Mol Phylogenet Evol 77: 83–95

Ammerman LK, Brashear WA, Bartlett SN (2013) Further evidence for the basal divergence of *Cheiromeles* (Chiroptera: Molossidae). Acta Chiropt 15(2): 307–312

Ammerman LK, Hillis DM (1992) A molecular test of bat relationships: monophyly or diphyly? Syst Biol 41(2): 222–232

Ammerman LK, Lee DN, Tipps TM (2012) First molecular phylogenetic insights into the evolution of free-tailed bats in the subfamily Molossinae (Molossidae, Chiroptera). J Mammal 93(1): 12–28

Andersen K (1912) Catalogue of the Chiroptera in the collection of the British museum, volume I: Megachiroptera, 2nd edn. British Museum (Natural History), London, 854 pp

Appleton BR, McKenzie JA, Christidis L (2004) Molecular systematics and biogeography of the bent-wing bat complex *Miniopterus schreibersii* (Kuhl, 1817)(Chiroptera: Vespertilionidae). Mol Phylogenet Evol 31(2): 431–439

Archibald JD, Deutschman DH (2001) Quantitative analysis of the timing of the origin and diversification of extant placental orders. J Mammal Evol 8(2): 107–124

Bailey SE, Mao X, Struebig M, Tsagkogeorga G, Csorba G, Heaney LR, Rossiter SJ (2016) The use of museum samples for large-scale sequence capture: a study of congeneric horseshoe bats (family Rhinolophidae). Biol J Linn Soc 117(1): 58–70

Baird AB, Braun JK, Mares MA, Morales JC, Patton JC, Tran CQ, Bickham JW (2015) Molecular systematic revision of tree bats (Lasiurini): doubling the native mammals of the Hawaiian islands. J Mammal 96 (6): 1255–1274

Baker RJ, Bininda-Emonds OR, Mantilla-Meluk H, Porter CA, Van Den Bussche RA (2012) Molecular timescale of diversification of feeding strategy and morphology in New World leaf-nosed bats (Phyllostomidae): a phylogenetic perspective. In: Gunnell GF, Simmons NB (eds) Evolutionary History of Bats: Fossils, Molecules and Morphology. Cambridge University Press, Cambridge, pp 385–409

Baker RJ, Hoofer SR, Porter CA, Van Den Bussche RA (2003) Diversification among New World leaf-nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occas Papers Mus Texas Tech Univ 230(1): 1–32

Baker RJ, Solari S, Cirranello A, Simmons NB (2016) Higher level classification of phyllostomid bats with a summary of DNA synapomorphies. Acta Chiropt 18(1): 1–38

Bartlett SN, McDonough MM, Ammerman LK (2013) Molecular systematics of bonneted bats (Molossidae: *Eumops*) based on mitochondrial and nuclear DNA sequences. J Mammal 94(4): 867–880

Benda P, Vallo P (2009) Taxonomic revision of the genus *Triaenops* (Chiroptera: Hipposideridae) with description of a new species from southern Arabia and definitions of a new genus and tribe. Folia Zool 58: 1

Bergmans W (1997) Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 5. The genera *Lissonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899, and *Megaloglossus* Pagenstecher, 1885; general remarks and conclusions; annex: key to all species. Beaufortia 47: 11–90

Bilgin R, Gürün K, Maraci Ö, Furman A, Hulva P, Çoraman E, Horáček I (2012) Syntopic occurrence in Turkey supports separate species status for *Miniopterus schreibersii schreibersii* and *M. schreibersii pallidus* (Mammalia: Chiroptera). Acta Chiropt 14(2): 279–289

Bogdanowicz W, Owen RD (1998) In the Minotaur's labyrinth: phylogeny of the bat family Hipposideridae. In: Kunz TH, Racey PA (eds) Bat Biology and Conservation. Smithsonian Institution Press, Washington, D.C., pp 27–42

Borisenko AV, Kruskop SV, Ivanova NV (2008) A new mouse-eared bat (Mammalia: Chiroptera: Vespertilionidae) from Vietnam. Russ J Theriol 7(2): 57–69

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Comput Biol 10(4): e1003537. doi:10.1371/journal.pcbi.1003537

Butler PM, Greenwood M (1965) Insectivora and Chiroptera. In: Leakey LSB (ed) Olduvai Gorge 1951–1961, vol. 1, Fauna and Background. Cambridge University Press, Cambridge, pp 13–15

Butler PM, Hopwood AT (1957) Insectivora and Chiroptera from the Miocene rocks of Kenya colony. Fossil Mammals Afr 13:1–35

Carter AM, Goodman SM, Enders AC (2008) Female reproductive tract and placentation in sucker-footed bats (Chiroptera: Myzopodidae) endemic to Madagascar. Placenta 29:484–491

Castresana J (2002) Gblocks v. 0.91 b. online version available at: http://molevol. cmima. csic. es/castresana.

Chan LM, Goodman SM, Nowak MD, Weisrock DW, Yoder AD (2011) Increased population sampling confirms low genetic divergence among *Pteropus* (Chiroptera: Pteropodidae) fruit bats of Madagascar and other western Indian Ocean islands. PLoS Curr. doi:10.1371/currents.RRN1226

Cirranello A, Simmons NB, Solari S, Baker RJ (2016) Morphological diagnoses of higher-level phyllostomid taxa (Chiroptera: Phyllostomidae). Acta Chiropt 18(1): 39–71

Clare EL, Lim BK, Engstrom MD, Eger JL, Hebert PD (2007) DNA barcoding of Neotropical bats: species identification and discovery within Guyana. Mol Ecol 7(2): 184–190

Colgan DJ, Soheili S (2008) Evolutionary lineages in *Emballonura* and *Mosia* bats (Mammalia: Microchiroptera) from the southwestern Pacific. Pac Sci 62(2): 219–232

Cozzuol MA (2006) The Acre vertebrate fauna: age, diversity, and geography. J So Am Earth Sci 21:185–203

Csorba G (2011) A new species of *Glischropus* from the Indochinese subregion (Mammalia: Chiroptera: Vespertilionidae). Zootaxa 2925: 41–48

Csorba G, Bates PJ (2005) Description of a new species of *Murina* from Cambodia (Chiroptera: Vespertilionidae: Murininae). Acta Chiropt 7(1): 1–7

Csorba G, Chou CH, Ruedi M, Görföl T, Motokawa M, Wiantoro S, Furey N (2014) The reds and the yellows: a review of Asian *Chrysopteron* Jentink 1910 (Chiroptera: Vespertilionidae: *Myotis*). J Mammal 95(4): 663–678

Csorba G, Görföl T, Wiantoro S, Kingston T, Bates PJ, Huang JCC (2015) Thumb-pads up—a new species of thick-thumbed bat from Sumatra (Chiroptera: Vespertilionidae: *Glischropus*). Zootaxa 3980(2): 267–278

Csorba G, Son NT, Saveng I, Furey NM (2011) Revealing cryptic bat diversity: three new *Murina* and redescription of *M. tubinaris* from Southeast Asia. J Mammal 92(4): 891–904

Csorba G, Ujhelyi P, Thomas N (2003) Horseshoe Bats of the World (Chiroptera: Rhinolophidae). Alana Books, Shropshire

Czaplewski NJ (1996) Opossums (Didelphidae) and bats (Noctilionidae and Molossidae) from the late Miocene of the Amazon basin. J Mammal 77:84–94

Czaplewksi NJ, Cartelle C (1998) Pleistocene bats from cave deposits in Bahia, Brazil. J Mammal 79:784–803

Czaplewski NJ, Peachey WD (2003) Late Pleistocene bats from Arkenstone cave, Arizona. Southwest Nat 48:597–609

Czaplewski NJ, Rincón AD, Morgan GS (2005) Fossil bat (Mammalia: Chiroptera) remains from Inciarte Tar Pit, Sierra de Perijá, Venezuela. Caribb J Sci 41:768–781

Czaplewski NJ, Takai M, Naeher TM, Shigehara N, Setoguchi T (2003b) Additional bats from the middle Miocene La Venta Fauna of Colombia. Rev Acad Colomb Cienc 27: 263–282

Čermák S, Wagner J, Fejfar O, Horáček I (2007) New Pliocene localities with micromammals from the Czech Republic: a preliminary report. Fossil Rec 10:60–68

dos Reis M, Inoue J, Hasegawa M, Asher RJ, Donoghue PC, Yang Z (2012) Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. Proc R Soc Lond [Biol] 279**:** 3491–3500

Dalquest WW (1978) Early Blancan mammals of the Beck Ranch Local Fauna of Texas. J Mammal 59: 269–298

Dalquest WW, Roth E (1970) Late Pleistocene mammals from a cave in Tamaulipas, Mexico. Southwest Nat 15: 217–230

Datzmann T, von Helversen O, Mayer F (2010) Evolution of nectarivory in phyllostomid bats (Phyllostomidae gray, 1825, Chiroptera: Mammalia). BMC Evol Biol 10: 165

Dávalos LM (2005) Molecular phylogeny of funnel-eared bats (Chiroptera: Natalidae), with notes on biogeography and conservation. Mol Phylogenet Evol 37(1): 91–103

Dávalos LM (2006) The geography of diversification in the mormoopids (Chiroptera: Mormoopidae). Biol J Linn Soc 88(1): 101–118

Dolman RW, Ammerman LK (2015) Molecular systematics of *Nyctinomops* (Chiroptera: Molossidae). West N Am Naturalist 75(1): 43–51

Dumont ER, Dávalos LM, Goldberg A, Santana SE, Rex K, Voigt CC (2011) Morphological innovation, diversification and invasion of a new adaptive zone. Proc R Soc Lond [Biol] 279: 1797–1805

Eick GN, Jacobs DS, Matthee CA (2005) A nuclear DNA phylogenetic perspective on the evolution of echolocation and historical biogeography of extant bats (Chiroptera). Mol Biol Evol 22(9): 1869–1886

Eiting TP, Gunnell GF (2009) Global completeness of the bat fossil record. J Mammal Evol 16(3): 151–173

Engesser B, Ziegler R (1996) Didelphids, insectivores, and chiropterans from the later Miocene of France, Cental Europe, Greece, and Turkey. In: Bernor RL, Fahlbusch V, Mittman H-W (eds) The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York, pp 157–167

Esselstyn JA (2007) A new species of stripe-faced fruit bat (Chiroptera: Pteropodidae: *Styloctenium*) from the Philippines. J Mammal 88(4): 951–958

Esselstyn JA, Garcia HJ, Saulog MG, Heaney LR (2008) A new species of *Desmalopex* (Pteropodidae) from the Philippines, with a phylogenetic analysis of the Pteropodini. J Mammal 89(4): 815–825

Fabre PH, Hautier L, Dimitrov D, Douzery EJ (2012) A glimpse on the pattern of rodent diversification: a phylogenetic approach. BMC Evol Biol 12(1): 88

Foley NM, Thong VD, Soisook P, Goodman SM, Armstrong KN, Jacobs DS, Teeling EC (2015) How and why overcome the impediments to resolution: lessons from rhinolophid and hipposiderid bats. Mol Biol Evol 32(2): 313–333

Furey NM, Thong VD, Bates PJ, Csorba G (2009) Description of a new species belonging to the *Murina'suilla*-group' (Chiroptera: Vespertilionidae: Murininae) from North Vietnam. Acta Chiropt 11(2): 225–236

Furman A, Postawa T, Öztunç T, Çoraman E (2010) Cryptic diversity of the bent-wing bat, *Miniopterus schreibersii* (Chiroptera: Vespertilionidae), in Asia minor. BMC Evol Biol 10(1): 121

Giannini NP (2012) Toward an integrative theory on the origin of bat flight. In: Gunnell GF, Simmons NB (eds) Evolutionary History of Bats. Cambridge University Press, Cambridge, pp 355–384

Giannini NP, Almeida FC, Simmons NB (2009) Phylogenetic relationships of harpyionycterine megabats. Bull Am Mus Nat Hist 331: 183–204

Giannini NP, Almeida FC, Simmons NB, DeSalle R (2006) Phylogenetic relationships of the enigmatic harpy fruit bat, *Harpyionycteris* (Mammalia: Chiroptera: Pteropodidae). Am Mus Novitates 1–12

Giannini NP, Almeida FC, Simmons NB, Helgen KM (2008) The systematic position of *Pteropus leucopterus* and its bearing on the monophyly and relationships of *Pteropus* (Chiroptera: Pteropodidae). Acta Chiropt 10(1): 11–20

Giannini NP, Simmons NB (2003) A phylogeny of megachiropteran bats (Mammalia: Chiroptera: Pteropodidae) based on direct optimization analysis of one nuclear and four mitochondrial genes. Cladistics 19(6): 496–511

Giannini NP, Simmons NB (2005) Conflict and congruence in a combined DNA–morphology analysis of megachiropteran bat relationships (Mammalia: Chiroptera: Pteropodidae). Cladistics 21(5): 411–437

Gingerich PD (1977) Radiation of Eocene Adapidae in Europe. Geobios 10: 165–182

Goloboff PA (1999) Analyzing large datasets in reasonable times: solutions for composite optima. Cladistics 15(4): 415–428

Goloboff PA, Catalano SA (2012) GB-to-TNT: facilitating creation of matrices from GenBank and diagnosis of results in TNT. Cladistics 28(5): 503–513

Goloboff P, Farris J, Nixon K (2003) TNT: tree analysis using new technology. Program and documentation available from the authors and at http://www.zmuc.dk/public/phylogeny/tnt

Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. Cladistics 24(5): 774–786

Goodman SM, Puechmaille SJ, Friedli-Weyeneth N, Gerlach J, Ruedi M, Schoeman MC, Stanley WT, Teeling EC (2012) Phylogeny of the emballonurini (Emballonuridae) with descriptions of a new genus and species from Madagascar. J Mammal 93(6): 1440–1455

Gregorin R (2009) Phylogeny of *Eumops* miller, 1906 (Chiroptera: Molossidae) using morphological data. Acta Chiropt 11(2): 247–258

Gregorin R, Cirranello A (2015) Phylogeny of Molossidae Gervais (Mammalia: Chiroptera) inferred by morphological data. Cladistics 1–34

Gregorin R, Ditchfield AD (2005) New genus and species of nectar-feeding bat in the tribe Lonchophyllini (Phyllostomidae: Glossophaginae) from northeastern Brazil. J Mammal 86(2): 403–414

Gregorin R, Gonçalves E, Lim BK, Engstrom MD (2006) New species of disk-winged bat *Thyroptera* and range extension for *T. discifera*. J Mammal 87(2): 238–246

Gregory WK (1910) The orders of mammals. Bull Am Mus Nat Hist 27: 1–542

Griffiths TA (1994) Phylogenetic systematics of slit-faced bats (Chiroptera, Nycteridae), based on hyoid and other morphology. Am Mus Novitates 3090: 1–17

Griffiths TA (1997) Phylogenetic position of the bat *Nycteris javanica* (Chiroptera: Nycteridae). J Mammal 78(1): 106–116

Griffiths TA, Smith AL (1991) Systematics of emballonuroid bats (Chiroptera, Emballonuridae and Rhinopomatidae), based on hyoid morphology. Bull Am Mus Nat Hist 206: 62–83

Guillén-Servent A, Francis CM (2006) A new species of bat of the *Hipposideros bicolor* group (Chiroptera: Hipposideridae) from central Laos, with evidence of convergent evolution with Sundaic taxa. Acta Chiropt 8(1): 39–61

Guillén-Servent A, Francis CM, Ricklefs RE (2003) Phylogeny and biogeography of the horseshoe bats. In: Thomas N, Csorba G, Ujhelyi P (eds) Horseshoe Bats of the World. Alana Books, pp. 12–24

Gunnell GF, Simmons NB (2005) Fossil evidence and the origin of bats. J Mammal Evol 12: 209–246

Gunnell GF, Simmons NB, Seiffert ER (2014) New Myzopodidae (Chiroptera) from the late Paleogene of Egypt: emended family diagnosis and biogeographic origins of Noctilionoidea. PLoS One. doi:10.1371/journal.pone.0086712

Gunnell GF, Simons EL, Seiffert ER (2008) New bats (Mammalia: Chiroptera) from the late Eocene and early Oligocene, Fayum depression, Egypt. J Vertebr Paleontol 28:1–11

Handley CO (1959) A revision of bats of the Genera *Euderma* and *Plecotus*. Smithsonian Institution Press, Washington

Hassanin A (2014) Description of a new bat species of the tribe Scotonycterini (Chiroptera, Pteropodidae) from southwestern Cameroon. C R Biol 337(2): 134–142

Hassanin A, Khouider S, Gembu GC, Goodman SM, Kadjo B, Nesi N, Pourrut X, Nakouné E, Bonillo C (2015) The comparative phylogeography of fruit bats of the tribe Scotonycterini (Chiroptera, Pteropodidae) reveals cryptic species diversity related to African Pleistocene forest refugia. C R Biol 338(3):197–211. doi:10.1016/j.crvi.2014.12.003

Havird JC, Miyamoto MM (2010) The importance of taxon sampling in genomic studies: an example from the cyclooxygenases of teleost fishes. Mol Phylogenet Evol 56(1): 451–455

Hill JE (1963) A revision of the genus *Hipposideros*. Bull Br Mus Nat Hist 11: 3–129

Hoffmann FG, Hoofer SR, Baker RJ (2008) Molecular dating of the diversification of phyllostominae bats based on nuclear and mitochondrial DNA sequences. Mol Phylogenet Evol 49(2): 653–658

Hollar LJ, Springer MS (1997) Old World fruitbat phylogeny: evidence for convergent evolution and an endemic African clade. Proc Natl Acad Sci USA 94(11): 5716–5721

Hoofer SR, Van Den Bussche RA (2001) Phylogenetic relationships of plecotine bats and allies based on mitochondrial ribosomal sequences. J Mammal 82(1): 131–137

Hoofer SR, Van Den Bussche RA (2003) Molecular phylogenetics of the chiropteran family Vespertilionidae. Acta Chiropt 5(1): 1–63

Horáček I (1986) *Kerivoula* (Mammalia, Chiroptera), fossil in Europe? Acta Univ Carolinae-Geol, Špinar 2: 213–222

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, Hanák V, Gaisler J (2000) Bats of the palearctic region: a taxonomic and biogeographic review. Proceedings of the VIII European Bats Research Symposium: 11–157

Hulva P, Horáček I, Benda P (2007) Molecules, morphometrics and new fossils provide an integrated view of the evolutionary history of Rhinopomatidae (Mammalia: Chiroptera). BMC Evol Biol 7(1): 1

Hurtado-Miranda NE, Pacheco-Torres V (2014) Análisis filogenético del género *Mimon* Gray, 1847 (Mammalia, Chiroptera, Phyllostomidae) con la descripción de un nuevo género. Therya 5(3): 751–791

Hutcheon JM, Kirsch JA (2004) Camping in a different tree: results of molecular systematic studies of bats using DNA–DNA hybridization. J Mammal Evol 11(1) 17–47

Hutcheon JM, Kirsch JA (2006) A moveable face: deconstructing the Microchiroptera and a new classification of extant bats. Acta Chiropt 8(1): 1–10

Hutcheon JM, Kirsch JA, Pettigrew JD (1998) Base–compositional biases and the bat problem III. The question of microchiropteran monophyly. Phil Trans R Soc Lond [Biol] 353(1368): 607–617

Hutson AM, Aulagnier S, Benda P, Karataş A, Palmeirim J, Paunović M (2008) *Miniopterus schreibersii*. The IUCN Red List of Threatened Species 2008: e.T13561A4160556. doi:10.2305/IUCN.UK.2008.RLTS.T13561A4160556.en

Jones KE, Bininda-Emonds OR, Gittleman JL (2005) Bats, clocks, and rocks: diversification patterns in Chiroptera. Evolution 59(10): 2243–2255

Juste J, Ferrández A, Fa JE, Masefield W, Ibáñez C (2007) Taxonomy of little bent-winged bats (*Miniopterus*, Miniopteridae) from the African islands of Sao Tomé, grand Comoro and Madagascar, based on mtDNA. Acta Chiropt 9(1): 27–37

Juste J, Álvarez Y, Tabarez E, Garrido-Pertierra A, Ibañez C, Bautista JM (1999) Phylogeography of African fruitbats (Megachiroptera). Mol Phylogenet Evol 13: 596–604

Juste J, Benda P, García-Mudarra JL, Ibáñez C (2013) Phylogeny and systematics of Old World serotine bats (genus *Eptesicus*, Vespertilionidae, Chiroptera): an integrative approach. Zool Scripta 42: 441–457

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30(4): 772–780

Kirsch JA, Hutcheon JM, Byrnes DG, Lloyd BD (1998) Affinities and historical zoogeography of the New Zealand short-tailed bat, *Mystacina tuberculata* gray 1843, inferred from DNA-hybridization comparisons. J Mammal Evol 5(1): 33–64

Koopman KF (1993) Order Chiroptera. In: Wilson DE, Reeder DM (eds) Mammal Species of the World: A Taxonomic and Geographic Reference, 2nd edn. Smithsonian Institution Press, Washington, D.C., pp 137–241

Koopman KF (1994) Chiroptera: Systematics. Handbuch der Zoologie, viii, Mammalia, part 60. Walter de Gruyter, Berlin, 216 pp

Kruskop SV, Borisenko AV, Ivanova NV, Lim BK, Eger JL (2012) Genetic diversity of northeastern Palaearctic bats as revealed by DNA barcodes. Acta Chiropt 14(1): 1–14

Kruskop SV, Eger JL (2008) A new species of tube-nosed bat *Murina* (Vespertilionidae: Chiroptera) from Vietnam. Acta Chiropt 10: 213–220

Kunz TH, Pierson ED (1994) Bats of the world: an introduction. In: Walker's Bats of the World. Johns Hopkins University Press, Baltimore and London, pp 1–46

Kuo HC, Fang YP, Csorba G, Lee LL (2009) Three new species of *Murina* (Chiroptera: Vespertilionidae) from Taiwan. J Mammal 90(4): 980–991

Lack JB, Roehrs ZP, Stanley CE Jr, Ruedi M, Van Den Bussche RA (2010) Molecular phylogenetics of *Myotis* indicates familial-level divergence for the genus *Cistugo* (Chiroptera). J Mammal 91(4): 976–992

Lack JB, Van Den Bussche RA (2010) Identifying the confounding factors in resolving phylogenetic relationships in Vespertilionidae. J Mammal 91(6): 1435–1448

Lamb JM, Ralph TM, Naidoo T, Taylor PJ, Ratrimomanarivo F, Stanley WT, Goodman SM (2011) Toward a molecular phylogeny for the Molossidae (Chiroptera) of the Afro-Malagasy region. Acta Chiropt 13(1): 1–16

Larsen PA, Hoofer SR, Bozeman MC, Pedersen SC, Genoways HH, Phillips CJ, Baker RJ (2007) Phylogenetics and phylogeography of the *Artibeus jamaicensis* Complex based on cytochrome-b DNA sequences. J Mammal 88(3): 712–727

Larsen RJ, Knapp MC, Genoways HH, Khan FAA, Larsen PA, Wilson DE, Baker RJ (2012) Genetic diversity of Neotropical *Myotis* (Chiroptera: Vespertilionidae) with an emphasis on South American species. PLoS One. doi:10.1371/journal.pone.0046578

Legendre S (1980) Un chiroptère emballonuridé dans le néogène d'Europe occidentale; considerations paléobio- géographiques. Géobios 13: 839–847

Legendre S (1982) Hipposideridae (Mammalia: Chiroptera) from the Mediterranean middle and late Neogene, and evolution of the genera *Hipposideros* and *Asellia*. J Vertebr Paleontol 2(3): 372–385

Legendre S (1985) Molossidés (Mammalia, Chiroptera) cén- ozoïques de l'Ancien et du Nouveau Monde; statut systématique; integration phylogénique des données. N Jb Geol Paläont Abh 170: 205–227

Lewis-Oritt N, Van Den Bussche RA, Baker RJ (2001) Molecular evidence for evolution of piscivory in *Noctilio* (Chiroptera: Noctilionidae). J Mammal 82(3): 748–759

Li G, Liang B, Wang Y, Zhao H, Helgen K M, Lin L, Zhang S (2007) Echolocation calls, diet, and phylogenetic relationships of Stoliczka's trident bat, *Aselliscus stoliczkanus* (Hipposideridae). J Mammal 88(3): 736–744

Lim BK, Engstrom MD, Bickham JW, Patton JC (2008) Molecular phylogeny of New World sheath-tailed bats (Emballonuridae: Diclidurini) based on loci from the four genetic transmission systems in mammals. Biol J Linn Soc 93(1): 189–209

Lim BK, Engstrom MD, Lee TE Jr, Patton JC, Bickham JW (2004) Molecular differentiation of large species of fruit-eating bats (*Artibeus*) and phylogenetic relationships based on the cytochrome b gene. Acta Chiropt 6(1): 1–12

Maddison WP, Maddison DR (2015) Mesquite: a modular system for evolutionary analysis. Vesion 3.03.

Medina CE, Gregorin R, Zeballos H, Zamora HT, Moras LM (2014) A new species of *Eumops* (Chiroptera: Molossidae) from southwestern Peru. Zootaxa 3878(1): 19–36

Meredith RW, Janečka JE, Gatesy J, Ryder OA, Fisher CA, Teeling EC, Goodbla A, Eizirik E, Simão TLL, Stadler T, Rabosky DL, Honeycutt RL, Flynn JJ, Ingram CM, Steiner C, Williams TL, Robinson TJ, Burk-Herrick A, Westerman M, Ayoub NA, Springer MS, Murphy WJ (2011) Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. Science 334(6055): 521–524

Miller MA, Pfeiffer W, Schwartz T (2010) "Creating the CIPRES Science Gateway for inference of large phylogenetic trees" in Proceedings of the Gateway Computing Environments Workshop (GCE) 14 Nov 2010, New Orleans, pp 1–8

Miller-Butterworth CM, Eick G, Jacobs DS, Schoeman MC, Harley EH (2005) Genetic and phenotypic differences between south African long-fingered bats, with a global miniopterine phylogeny. J Mammal 86(6): 1121–1135

Miller-Butterworth CM, Murphy WJ, O'Brien SJ, Jacobs DS, Springer MS, Teeling EC (2007) A family matter: conclusive resolution of the taxonomic position of the long-fingered bats, *Miniopterus*. Mol Biol Evol 24(7): 1553–1561

Morgan GS (1991) Neotropical Chiroptera from the Pliocene and Pleistocene of Florida. Bull Am Mus Nat Hist 206: 176–213

Morgan GS, Czaplewski NJ (2003) A new bat (Chiroptera: Natalidae) from the early Miocene of Florida, with comments on natalid phylogeny. J Mammal 84:729–752

Morgan GS, Czaplewski NJ (2012) Evolutionary history of the Neotropical Chiroptera: the fossil record. In: Gunnell GF, Simmons NB (eds) Evolutionary History of Bats: Fossils, Molecules, and Morphology. Cambridge University Press, Cambridge, 105–161

Morgan GS, Linares OJ, Ray CE (1988) New species of fossil vampire bats (Mammalia: Chiroptera: Desmodontidae) from Florida and Venezuela. Proc Biol Soc Wash 101: 912–928

Murphy WJ, Eizirik E, Johnson WE, Zhang YP, Ryder OA, O'Brien SJ (2001) Molecular phylogenetics and the origins of placental mammals. Nature 409(6820): 614–618

Murray SW, Campbell P, Kingston T, Zubaid A, Francis CM, Kunz TH (2012) Molecular phylogeny of hipposiderid bats from Southeast Asia and evidence of cryptic diversity. Mol Phylogenet Evol 62(2): 597–611

Nabholz B, Glémin S, Galtier N (2008) Strong variations of mitochondrial mutation rate across mammals – the longevity hypothesis. Mol Biol Evol 25(1): 120–130

Nesi N, Kadjo B, Pourrut X, Leroy E, Shongo CP, Cruaud C, Hassanin A (2013) Molecular systematics and phylogeography of the tribe Myonycterini (Mammalia, Pteropodidae) inferred from mitochondrial and nuclear markers. Mol Phylogenet Evol 66(1): 126–137

Nishihara H, Hasegawa M, Okada N (2006) Pegasoferae, an unexpected mammalian clade revealed by tracking ancient retroposon insertions. Proc Natl Acad Sci USA 103(26): 9929–9934

O'Brien J, Mariani C, Olson L, Russell AL, Say L, Yoder AD, Hayden TJ (2009) Multiple colonisations of the western Indian Ocean by *Pteropus* fruit bats (Megachiroptera: Pteropodidae): the furthest islands were colonised first. Mol Phylogenet Evol 51(2): 294–303

O'Leary MA, Bloch JI, Flyinn JJ, Gaudin TJ, Giallombardo A, Giannini NP, Goldberg SL, Kraatz BP, Luo ZX, Meng J, Ni X, Novacek MJ, Perini FA, Randall ZS, Rougier GW, Sargis EJ, Silcox MT, Simmons NB, Spaulding M, Velazco PM, Weksler M, Wible JR, Cirranello AL (2013) The placental mammal ancestor and the post–K-Pg radiation of placentals. Science 339(6120): 662–667

Parlos JP, Timm RM, Swier VJ, Zeballos J, Baker RJ (2014) Evaluation of paraphyletic assemblages witihin Lonchophyllinae, with description of a new tribe and genus. Occas Pap Mus Texas Tech Univ 320: 1–23

Patton JC, Baker RJ (1978) Chromosomal homology and evolution of phyllostomatoid bats. Syst Biol 27(4): 449–462

Peel AJ, Sargan DR, Baker KS, Hayman DT, Barr JA, Crameri G, Suu-Ire R, Broder CC, Lembo T, Wang L-F, Fooks AR, Rossiter SJ, Wood JLN, Cunningham AA (2013) Continent-wide panmixia of an African fruit bat facilitates transmission of potentially zoonotic viruses. Nature 4:doi:10.1038/ncomms3770

Pettigrew JD (1986) Flying primates? Megabats have the advanced pathway from eye to midbrain. Science 231: 1304–1306

Pettigrew JD (1991a) Wings or brain? Convergent evolution in the origins of bats. Syst Zool 40: 199–216

Pettigrew JD (1991b) A fruitful, wrong hypothesis? Response to Baker, Novacek, and Simmons. Syst Biol 40: 231–239

Pick KS, Philippe H, Schreiber F, Erpenbeck D, Jackson DJ, Wrede P, Wiens M, Alié A, Morgenstern B, Manuel M, Wörheide G (2010) Improved phylogenomic taxon sampling noticeably affects nonbilaterian relationships. Mol Biol Evol 27(9): 1983–1987

Rambaut A (2014) FigTree v 1.4.2. http://tree.bio.ed.ac.uk/software/figtree/

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6, Available from http://beast.bio.ed.ac.uk/Tracer

Ray CE (1967) Pleistocene mammals from Ladds, Bartow County, Georgia. Bull Georgia Acad Sci 25: 120–150

Redondo RA, Brina LP, Silva RF, Ditchfield AD, Santos FR (2008) Molecular systematics of the genus *Artibeus* (Chiroptera: Phyllostomidae). Mol Phylogenet Evol 49(1): 44–58

Robbins LW, Sarich VM (1988) Evolutionary relationships in the family Emballonuridae (Chiroptera). J Mammal 69(1): 1–13

Robinson MF, Jenkins PD, Francis CM, Fulford AJ (2003) A new species of the *Hipposideros pratti* group (Chiroptera, Hipposideridae) from Lao PDR and Vietnam. Acta Chiropt 5(1): 31–48

Roehrs ZP, Lack JB, Van Den Bussche RA (2010) Tribal phylogenetic relationships within Vespertilioninae (Chiroptera: Vespertilionidae) based on mitochondrial and nuclear sequence data. J Mammal 91(5): 1073–1092

Roehrs ZP, Lack JB, Van Den Bussche RA (2011) A molecular phylogenetic reevaluation of the tribe Nycticeiini (Chiroptera: Vespertilionidae). Acta Chiropt 13(1): 17–31

Rojas D, Warsi OM, Dávalos LM (2016) Bats (Chiroptera: Noctilionoidea) challenge a recent origin of extant Neotropical diversity. Syst Biol 65(3): 432–448

Rossina VV, Kruskop SV, Tesakov AS, Titov VV (2006) The first record of late Miocene bat from European Russia. Acta Zool Cracov 49A: 125–133

Ruedi M, Csorba G, Lin LK, Chou CH (2015) Molecular phylogeny and morphological revision of *Myotis* bats (Chiroptera: Vespertilionidae) from Taiwan and adjacent China. Zootaxa 3920(1): 301–342

Ruedi M, Friedli-Weyeneth N, Teeling EC, Puechmaille SJ, Goodman SM (2012) Biogeography of Old World emballonurine bats (Chiroptera: Emballonuridae) inferred with mitochondrial and nuclear DNA. Mol Phylogenet Evol 64(1): 204–211

Ruedi M, Stadelmann B, Gager Y, Douzery EJP, Francis CM, Lin L-K, Guillén-Serven A, Cibois A (2013) Molecular phylogenetic reconstructions identify East Asia as the cradle for the evolution of the cosmopolitan genus *Myotis* (Mammalia, Chiroptera). Mol Phylogenet Evol 69: 437–449

Samonds KE (2007) Late Pleistocene bat fossils from Anjohibe cave, northwestern Madagascar. Acta Chiropt 9: 39–65

Schutt WA Jr, Simmons NB (1998) Morphology and homology of the chiropteran calcar, with comments on the phylogenetic relationships of *Archaeopteropus*. J Mammal Evol 5(1): 1–32

Shi JJ, Rabosky DL (2015) Speciation dynamics during the global radiation of extant bats. Evolution 69(6): 1528–1545

Sigé B (1968) Les chiropteres du Miocene inferieur de Bouzigues I Etude systematique. Palaeovertebrata 1(3): 65–133

Silva-Taboada G (1974) Fossil Chiroptera from cave deposits in central Cuba, with descriptions of two new species (genera *Pteronotus* and *Mormoops*) and the first west Indian record of *Mormoops megalophylla*. Acta Zool Cracov 19: 33–73

Simmons NB (1994) The case for chiropteran monophyly. Am Mus Novitates 3103: 1–54

Simmons NB (2005) Order Chiroptera. In: Wilson DE, Reeder DM (eds) Mammals Species of the World: A Taxonomic and Geographic Reference, 3rd edn. John Hopkins University Press, Baltimore, pp 312–529

Simmons NB, Conway TM (2001) Phylogenetic relationships of mormoopid bats (Chiroptera: Mormoopidae) based on morphological data. Bull Am Mus Nat Hist 258: 1–97

Simmons NB, Geisler JH (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. Bull Am Mus Nat Hist 235: 1–182

Simmons NB, Seymour KL, Habersetzer J, Gunnell GF (2008) Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. Nature 451: 818–822

Smith JD (1972) Systematics of the chiropteran family Mormoopidae. Misc Publ Mus Nat Hist Univ Kansas 56: 1–132

Smith T, Habersetzer J, Simmons NB, Gunnell GF (2012) Systematics and paleobiogeography of early bats. In: Gunnell GF, Simmons NB (eds) Evolutionary History of Bats. Cambridge University Press, Cambridge, pp 23–66

Soisook P, Karapan S, Satasook C, Bates P J (2013) A new species of *Murina* (Mammalia: Chiroptera: Vespertilionidae) from peninsular Thailand. Zootaxa 3746(4): 567–579

Solari S, Hoofer SR, Larsen PA, Brown AD, Bull RJ, Guerrero JA, Ortega J, Carrera JP, Bradley RD, Baker RJ (2009) Operational criteria for genetically defined species: analysis of the diversification of the small fruit-eating bats, *Dermanura* (Phyllostomidae: Stenodermatinae). Acta Chiropt 11(2): 279–288

Son NT, Csorba G, Tu VT, Thong VD, Wu Y, Harada M, Motokawa M (2015) A new species of the genus *Murina* (Chiroptera: Vespertilionidae) from the central highlands of Vietnam with a review of the subfamily Murininae in Vietnam. Acta Chiropt 17(2): 201–232

Springer MS, Stanhope MJ, Madsen O, de Jong WW (2004) Molecules consolidate the placental mammal tree. Trends Ecol Evol 19(8): 430–438

Stadelmann B, Lin L-K, Kunz TH, Ruedi M (2007) Molecular phylogeny of the New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. Mol Phylogenet Evol 43: 32–48

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. Syst Biol 57(5): 758–771

Stoffberg S, Jacobs DS, Mackie IJ, Matthee CA (2010) Molecular phylogenetics and historical biogeography of *Rhinolophus* bats. Mol Phylogenet Evol 54(1): 1–9

Storch G, Sigé B, Habersetzer J (2002) *Tachypteron franzeni* n. Gen., n. Sp., earliest emballonurid bat from the middle Eocene of Messel (Mammalia, Chiroptera). Paläontol Z 76(2): 189–199

Suárez W, Díaz-Franco S (2003) A new fossil bat (Chiroptera: Phyllostomidae) from a quaternary cave deposit in Cuba. Caribb J Sci 39: 371–377

Sudman PD, Barkley LJ, Hafner MS (1994) Familial affinity of *Tomopeas ravus* (Chiroptera) based on protein electrophoretic and cytochrome b sequence data. J Mammal 75(2): 365–377

Talavera G, Castresana J (2007) Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. Syst Biol 56(4): 564–577

Teeling EC (2009) Hear, hear: the convergent evolution of echolocation in bats? Trends Ecol Evol 24(7): 351–354

Teeling EC, Dool S, Springer MS (2012) Phylogenies, fossils and functional genes: the evolution of echolocation in bats. In: Gunnell GF, Simmons NB (eds) Evolutionary History of Bats. Cambridge University Press, Cambridge, pp 1–22

Teeling EC, Scally M, Kao DJ, Romagnoli ML, Springer MS, Stanhope MJ (2000) Molecular evidence regarding the origin of echolocation and flight in bats. Nature 403(6766): 188–192

Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. Science 307(5709): 580–584

Tejedor A (2011) Systematics of funnel-eared bats (Chiroptera: Natalidae). Bull Am Mus Nat Hist 353:1–140

Tejedor A, Tavares VDC, Silva-Taboada G (2005) A revision of extant greater Antillean bats of the genus *Natalus*. Am Mus Novitates 1–22

Thabah A, Li G, Wang Y, Liang B, Hu K, Zhang S, Jones G (2007) Diet, echolocation calls, and phylogenetic affinities of the great evening bat (*Ia io*; Vespertilionidae): another carnivorous bat. J Mammal 88(3): 728–735

Thoisy BD, Pavan AC, Delaval M, Lavergne A, Luglia T, Pineau K, Catzeflis F (2014) Cryptic diversity in common mustached bats *Pteronotus* cf. *parnellii* (Mormoopidae) in French Guiana and Brazilian Amapa. Acta Chiropt 16(1): 1–13

Thong VD, Puechmaille SJ, Denzinger A, Bates PJ, Dietz C, Csorba G, Soisook P, Teeling EC, Matsumura S, Furey N, Schnitzler HU (2012a) Systematics of the *Hipposideros turpis* Complex and a description of a new subspecies from Vietnam. Mammal Rev 42(2): 166–192

Thong VD, Puechmaille SJ, Denzinger A, Csorba G, Dietz C, Bates PJ, Teeling EC, Schnitzler HU (2012b) A new species of *Hipposideros* (Chiroptera: Hipposideridae) from Vietnam. J Mammal 93(1): 1–11

Topál G (1983) New and rare fossil mouse-eared bats from the middle Pliocene of Hungary (Mammalia, Chiroptera). Fragm Mineral Palaeontol 11:43–54

Topál G (1989a) New Tertiary plecotines from Hungary (Mammalia, Chiroptera). In: Hanák V, Horáček I, Gaisler J (eds) European Bat Research 1987. Charles University Press, Prague, pp 77–86

Topál G (1989b) Tertiary and early Quaternary remains of *Corynorhinus* and *Plecotus* from Hungary (Mammalia, Chiroptera). Vertebr Hung 23:33–55

Tsagkogeorga G, Parker J, Stupka E, Cotton JA, Rossiter SJ (2013) Phylogenomic analyses elucidate the evolutionary relationships of bats. Curr Biol 23(22): 2262–2267

Tu VT, Csorba G, Görföl, Arai S, Son NT, Thanh HT, Hasanin A (2015) Description of a new species of the genus *Aselliscus* (Chiroptera, Hipposideridae) from Vietnam. Acta Chiropt 17(2): 233–254

Vahtera V, Edgecombe GD, Giribet G (2013) Phylogenetics of scolopendromorph centipedes: can denser taxon sampling improve an artificial classification? Invertebr Syst 27(5): 578–602

Van Den Bussche RA, Hoofer SR, Simmons NB (2002) Phylogenetic relationships of mormoopid bats using mitochondrial gene sequences and morphology. J Mammal 83(1): 40–48

Van Den Bussche RA, Hudgeons JL, Baker RJ (1998) Phylogenetic accuracy, stability, and congruence: relationships within and among the New World Bat genera *Artibeus*, *Dermanura*, and *Koopmania*. In: Kunz TH, Racey PA (eds) Bat Biology and Conservation. Smithsonian Institution Press, Washington, D.C., pp 59–71

Van Den Bussche RA, Weyandt SE (2003) Mitochondrial and nuclear DNA sequence data provide resolution to sister-group relationships within *Pteronotus* (Chiroptera: Mormoopidae). Acta Chiropt 5(1): 1–13

Velazco PM (2005) Morphological phylogeny of the bat genus *Platyrrhinus* Saussure, 1860 (Chiroptera: Phyllostomidae) with the description of four new species. Fieldiana Zool 1–53

Velazco PM (2013) On the phylogenetic position of *Carollia manu* Pacheco et al., 2004 (Chiroptera: Phyllostomidae: Carolliinae). Zootaxa 3718: 267–276

Velazco PM, Cadenillas R, Centty O, Huamani L, Zamora H (2013) New records of *Platalina genovensium* Thomas, 1928 (Chiroptera, Phyllostomidae, Lonchophyllinae) and *Tomopeas ravus* miller, 1900 (Chiroptera, Molossidae, Tomopeatinae). Mastozool Neotrop 20: 425–434

Velazco PM, Gregorin R, Voss RS, Simmons NB (2014) Extraordinary local diversity of disk-winged bats (Thyropteridae: *Thyroptera*) in northeastern Peru, with the description of a new species and comments on roosting behavior. Am Mus Novitates 3795 1–28

Velazco PM, Patterson BD (2013) Diversification of the yellow-shouldered bats, genus *Sturnira* (Chiroptera, Phyllostomidae), in the New World tropics. Mol Phylogenet Evol 68(3): 683–698

Volleth M (2013) Of bats and molecules: chromosomal characters for judging phylogenetic relationships. In: Adams RA, Pedersen SC (eds) Bat Evolution, Ecology, and Conservation, Springer, New York, pp 129–146

Volleth M, Loidl J, Mayer F, Yong HS, Müller S, Heller KG (2015) Surprising genetic diversity in *Rhinolophus luctus* (Chiroptera: Rhinolophidae) from peninsular Malaysia: description of a new species based on genetic and morphological characters. Acta Chiropt 17(1): 1–20

Wesselmann HB (1984) The Omo Micromammals. Systematics and Paleoecology of Early Man Sites from Ethiopia. Karger, New York

Wetterer AL, Rockman MV, Simmons NB (2000) Phylogeny of phyllostomid bats (Mammalia: Chiroptera): data from diverse morphological systems, sex chromosomes, and restriction sites. Bull Am Mus Nat Hist 248:1–200

Wilkinson GS, South JM (2002) Life history, ecology, and longevity in bats. Aging cell 1: 124–131

Wilson JJ, Sing KW, Halim MRA, Ramli R, Hashim R, Sofian-Azirun M (2014) Utility of DNA barcoding for rapid and accurate assessment of bat diversity in Malaysia in the absence of formally described species. Genet Mol Res 13(1): 920–925

Zhou ZM, Guillén-Servent A, Lim BK, Eger JL, Wang YX, Jiang XL (2009) A new species from southwestern China in the afro-Palearctic lineage of the horseshoe bats (*Rhinolophus*). J Mammal 90(1): 57–73

Ziegler R (2003) Bats (Chiroptera, Mammalia) from middle Miocene karstic fissure fillings of Petersbuch near Eichstätt, southern Franconian Alb (Bavaria). Geobios 36(4): 447–490

Zwickl DJ, Hillis DM (2002) Increased taxon sampling greatly reduces phylogenetic error. Syst Biol 51(4): 588–598