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Article *in* PLoS Currents · February 2011

DOI: 10.1371/currents.RRN1212 · Source: PubMed

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A time-calibrated species-level phylogeny of bats (Chiroptera, Mammalia)

February 4, 2011 · Tree of Life

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Abstract

Despite their obvious utility, detailed species-level phylogenies are lacking for many groups, including several major mammalian lineages such as bats. Here we provide a cytochrome b genealogy of over 50% of bat species (648 terminal taxa). Based on prior analyzes of related mammal groups, cytb emerges as a particularly reliable phylogenetic marker, and given that our results are broadly congruent with prior knowledge, the phylogeny should be a useful tool for comparative analyzes. Nevertheless, we stress that a single-gene analysis of such a large and old group cannot be interpreted as more than a crude estimate of the bat species tree. Analysis of the full dataset supports the traditional division of bats into macro- and microchiroptera, but not the recently proposed division into Yinpterochiroptera and Yangochiroptera. However, our results only weakly reject the former and strongly support the latter group, and furthermore, a time calibrated analysis of a pruned dataset where most included taxa have the entire 1140bp cytb sequence finds monophyletic Yinpterochiroptera. Most bat families and many higher level groups are supported, however, relationships among families are in general weakly supported, as are many of the deeper nodes of the tree. The exceptions are in most cases apparently due to the misplacement of species with little available data, while in a few cases the results suggest putative problems with current classification, such as the non-monophyly of Mormoopidae. We provide this phylogenetic hypothesis, and an analysis of divergence times, as tools for evolutionary and ecological studies that will be useful until more inclusive studies using multiple loci become available.

Introduction

Phylogenies form the backbone of evolutionary biology and represent tools that underlie a broad spectrum of evolutionary and ecological studies [1] [2]. Phylogenetic work on any given group often first focuses on the ‘big picture’, that is the placement of, and relationship among, major groups, long before species level phylogenies become available. One simple reason for this focus is that general interest questions, such as where and how the major divisions of life fit together, can be answered through sampling relatively few taxa, in a relatively cost and time effective manner. Yet, more detailed species-level phylogenies, often lagging far behind, are the most useful tools for evolutionary and ecological analyses. The above is certainly true for mammalian phylogenetics, where higher level phylogenetics are intensely studied, with the few detailed species level studies for major groups lagging far behind (see e.g. [3] [4] [5] [6]).

The ultimate goal of phylogenetics must be detailed species level phylogenies of all of life, based on many data. However, achieving this goal will take much time and effort. In the meantime, species level phylogenies may be rapidly reconstructed with already available data using several approaches. One is the construction of phylogenetic supertrees where available trees and taxonomies are united into a summary cladogram [7]. Another is the creation of supermatrices based on available character data. Both approaches make available useful research tools, which may have different strengths.

The bats (Chiroptera) are one such group where many phylogenetic studies have focused either on understanding higher-level bat relationships (e.g. [8] [9]) or species-level relationships within specific groups (e.g. [10] [11] [12]). Available phylogenies have then been summarized in a supertree [13]. Here, we provide cytochrome b gene tree for over 50% of bat species (648 total taxa). Cytb not only is the most widely available marker for most mammals, but also has been shown to be a particularly reliable phylogenetic marker (e.g. [14]). Thus according with prior analyses of other mammal groups [3] [4] [5] [6], the cytb gene tree can be expected to at least roughly approximate the species-level phylogeny of Chiroptera. We provide this phylogeny simply as an alternative tool to super-tree phylogenies, until more detailed studies become available.

Methods

Cytochrome b sequences were downloaded from GenBank for 648 bats, including nearly 550 named species, and the remaining terminal taxa being subspecies or unidentified/undescribed species. As outgroups we selected 10 species representing other Pegasoferae [15]: Cetartidoactyla, Perissodactyla, Carnivora, Pholidota (pangolins), and Erinaceomorpha as the primary outgroup. Because many of the taxa have incomplete Cytb sequences, and missing data can cause problems in phylogenetic reconstruction (e.g. [16]), we also created a 'pruned' dataset where taxa with less than 30% of the full sequence were removed ('pruned' matrix), and another set where only 2 representatives of each family were retained ('time' matrix). The latter was used for analysis of divergence times. The sequences were aligned in Mesquite [17], a trivial task given that it is a protein-coding gene with no implied gaps. The appropriate model for the Bayesian analysis was selected with jModeltest [18] using the AIC criterion [19]. The best model was GTR+Γ+I [20] [21]. Bayesian analysis was performed using MrBayes V3.1.2 [22] with settings as in [3] [4] with separate model estimation for first, second, and third codon positions. The MCMC was run with one cold and three heated chains for 30,000,000 generations, sampling trees every 1,000 generations. The first 15,000,000 were then discarded as burnin, after which stationarity was reached. The data matrix and trees are available from the first author and data and trees will be submitted to Treebase (http://www.treebase.org). Genbank accession numbers are listed in Table 1 (see Appendices).

The 'time' matrix was used to estimate divergence times using relaxed clock methods in BEAST 1.6.1. [23] [24]. For Emballonuridae we additionally retained two *Taphozous* species as these did not group with the other Emballonuridae in the full analysis. The analysis was calibrated using normally distributed priors reflecting: (1) the minimal age of 37 my for the split between Rhinolophidae and Hipposiderids based on the estimated age of the oldest rhinolophid and hipposiderid fossils [25] [26]; (2) the estimated age of Carnivora (split of cat plus dog) of 54 my (the age of Carnivora as estimated by [27]); the estimated age of Chiroptera as a normally distributed prior with mean of 54 my, also based on [27]; and (4) the minimal age of Emballonuridae of 48 my based on the oldest fossils that are with some certainty placed within that family [28]. Prior to the divergence time analysis *Erinaceus* (Erinaceomorpha) and *Talpa* (Eulipotyphla) were set as primary outgroups by enforcing the monophyly of the remaining taxa, and the monophyly of Rhinolopidae plus Hipposideridae was furthermore enforced. The resulting age estimates were then compared to the above mentioned fossil data in addition to the age of other known fossil bats [28].

Results and Discussion

Phylogenetics

The analysis of the full dataset supports the monophyly of bats, and the major division of Chiroptera into Megachiroptera (Pteropodidae) and Microchiroptera with Yangochiroptera contained within the latter group (Figures 1-2).

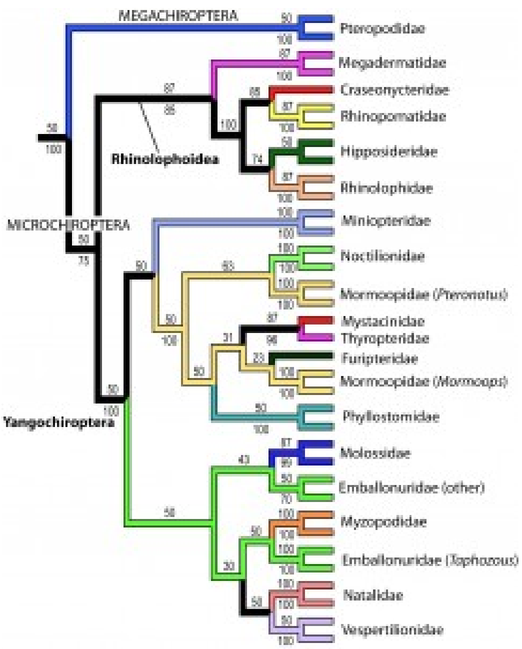

Fig. 1: Relationships among bat families according with the analysis of all data.

Numbers are posterior probabilities, above branches from the full analysis, below branches support from the pruned analysis.

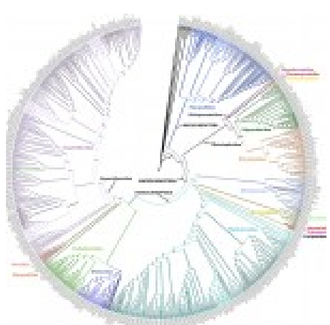

Fig. 2: Relationship among bat species with major clade names.

Numbers are posterior probabilities. The results are detailed in Figure 4, see Appendices.

The analysis of the 'time' matrix, however, supports the now rather generally accepted split into Yinpterochiroptera and Yangochiroptera (see below) (e.g. [29] [30] [31] [32] [33] [34]).

The Macrochiroptera, or fruitbats (Pteropodidae), are in the main analysis sister to the remaining bats (Figures 2, 4a). Within Pteropodidae most genera are monophyletic, with the exception of *Rousettus angolensis* (synonym *Lissonycterisangolensis*) nests with *Myonycteris* . Overall, these results are similar to results of previous studies on macrochiroptera phylogenetics (e.g. [10]).

The Microchiroptera is divided in two major clades, one is the Yangochiroptera including the families Emballonuridae, Furipteridae, Miniopteridae, Molossidae, Mormoopidae, Mystacinidae, Myzopodidae, Natalidae Noctilionidae, Phyllostomidae, Thyropteridae, and Vespertilionidae. The other major group, which we refer to as a modified "Rhinolophoidea" (Figures 1-2, 4), contains the remaining microbat families Craseonycteridae, Hipposideridae, Megadermatidae, Rhinolophidae, and Rhinopomatidae. Hipposideridae and Rhinolophidae are sister families as supported by previous studies (e.g., [13] [31] [34]). Only Hipposideridae here contains more than a single genus, and within that family *Hipposiderus* is paraphyletic, containing several small genera.

Overall most microchiropteran superfamilies are not supported as monophyletic, except Rhinopomatoidea (Figure 2). A modified Rhinolophoidea that contains Rhinopomatoidea is also supported, and the superfamily Vespertilionioidea is monophyletic except for containing a couple of apparently misplaced species (Figures 2, 4b). The relationships among the families, however, in general are poorly supported and differ among analyses (see Figures 1, 3-4). Taxonomic families are generally recovered either as strictly monophyletic, or approximately, as paraphyletic groups due to one or a couple of 'misplaced' taxa. In the full analysis, families that are strictly supported (i.e. monophyletic, or in the case of families represented by single species, not nesting within another family) are: Craseonycteridae, Furipteridae, Hipposideridae, Megadermatidae, Miniopteridae, Molossidae, Mystacinidae, Myzopodidae, Natalidae, Noctilionidae, Rhinolophidae, Rhinopomatidae, and Thyropteridae. Not monophyletic families are Phyllostomidae due to the placement of one *Platalina* species nesting within Vestpertilionidae, Emballonuridae is rendered polyphyletic by the placement of the genus *Taphozous* (2 species) and one species of *Emballonura* outside it. Vespertilionidae is paraphyletic in that within it are placed the above mentioned *Platalina* and *Emballonura*. Finally Mormoopidae forms two clades that are not sister, one including the genus *Mormoops*, the other the genus *Pteronotus*. These 'minor' deviations from family monophyly in most cases probably do not represent refutation of family clades; rather this seems to be mostly an issue of missing data. For example, when species with less than 30% of the sequence are removed, all families are recovered monophyletic, with two exceptions that may be taxonomically informative : (1) The genus *Taphozous* still groups outside Emballonuridae which contradicts previous studies (e.g., [32] [34] [35]) and (2) the Mormoopidae family still forms two separate clades, which agrees with Kennedy et al [36] (for contrasting topologies see e.g., [13] [31]). Finally, several genera of the family Phyllostomidae are not monophyletic, including *Mimon*, *Mycronycteris*, *Rousettus*, *Vampyressa*, and *Artibeus*. Within Molossidae *Tadarida*, *Mops*, *Chaerephon* are not monophyletic. Within Natalidae, *Chilonatalus* is non-monophyletic, and within Vespertilionidae, the large genera *Pipistrellus* and *Myotis* are not monophyletic.

Many taxa in the full analysis only have available a partial Cytb sequence, and notably clade support is low for many of the deeper clades of the phylogeny. Low support is unsurprising given missing data, and the use of only a single locus for both very many taxa and old divergences. Further, any given gene tree can be expected to differ from the species tree due to various processes including incomplete lineage sorting, introgression, and others. Thus, future effort should focus on resolving the species-level phylogeny of bats with a multi-locus approach. Nevertheless, the phylogeny, especially when the taxa with the highest % missing data are removed, is broadly congruent with prior knowledge, and should thus be a useful tool.

Divergence times

The analysis of divergence times (Figure 3) generally agrees with prior studies [27] [35] [37], though the estimated ages are rather lower in general than those estimated by Jones et al. [38].

Fig. 3: A calibrated phylogeny of bat families.

Numbers are in million years, and gray bars are 95% confidence intervals

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In part this may relate to the different suggested relationships among bat families across these studies, though the error margins of many nodes estimated are rather wide and nearly always include age estimates found by prior studies. The results also in most cases are consistent with the available bat fossil record [28]. The age of crown bats, i.e. the split between Yinpterochiroptera and Yangochiroptera is estimated at 58.9 my, a value lying in between the estimates of Cao et al. [27], and Jones et al. [38] and Arnason et al. [37]. Other dates that were included as priors, as expected, also are consistent with the fossil record. The split between Hipposideridae and Rhinolophidae is estimated at 36.9 my, consistent with the oldest known Hipposideridae fossil dated at close to 40 my. Similarly the age of Molossidae estimated at 36.1 my is close to the oldest Molossidae fossil at near 40 my [28]. The split between Emballonuridae and its sister lineage is estimated at 49 my, right around the age of the oldest emballonurid fossil. Most other dates are also consistent with the fossil record. The genus *Taphozous* has a fossil record going up to 20.4 my, a date in between the estimated split between crown *Taphozous* (18.1 my) and the split between *Taphozous* and other Emballonuridae (44.2 my). The oldest Mystacinidae fossil dates from around 20 my [28] and the estimated split here between Mystacinidae and its sister lineage is 24.3 my. The oldest Phyllostomidae fossil dates from around 16 my [28], a date in between the split between crown *Phyllostoma* (14.4 my) and the split between Phyllostomidae and its sister lineage (28.5 my). In a few cases the estimates are younger than possible given current understanding the fossil record, e.g. the age of Megadermatidae at 23.6 my while the oldest fossil is at least 37 my. However, 95% confidence interval of this node estimate reaches over 40 my. The age of Natalidae, estimated at around 43 my, is younger than the oldest fossil thought to belong to that family, at over 50 my. Similarly one putative Vespertilionidae genus, *Stehlinia*, has a fossil record older (up to 48 my) than the estimated age of the family at 36.1 my. These mismatches may reflect simply erroneous age estimates, or could possibly indicate that some fossil bats are taxonomically misplaced. In most other cases the estimated ages are older than the oldest available fossils, which may reflect the incompleteness of the fossil record.

In sum, we provide a *cytochrome b* genealogy for Chiroptera, which we expect to crudely approximate the bat species tree. Until more detailed species-level phylogenies become available, this offers an alternative phylogenetic tool to super-tree phylogenies, for comparative evolutionary, ecological analyzes, and phylogenetic conservation assessment.

Acknowledgments

Thanks to PLoS Currents: Tree of Life board of reviewers, the editor, and two anonymous reviewers for comments that improved this manuscript.

Funding information

This research was funded, in part, by the University of Puerto Rico. Competing interests The authors have declared that no competing interests exist.

Appendices

Figure 4. Results from Fig. 2 in standard tree format.

Figure 4a. Results from Figure 2, Pteropodidae. Numbers are posterior probabilities.

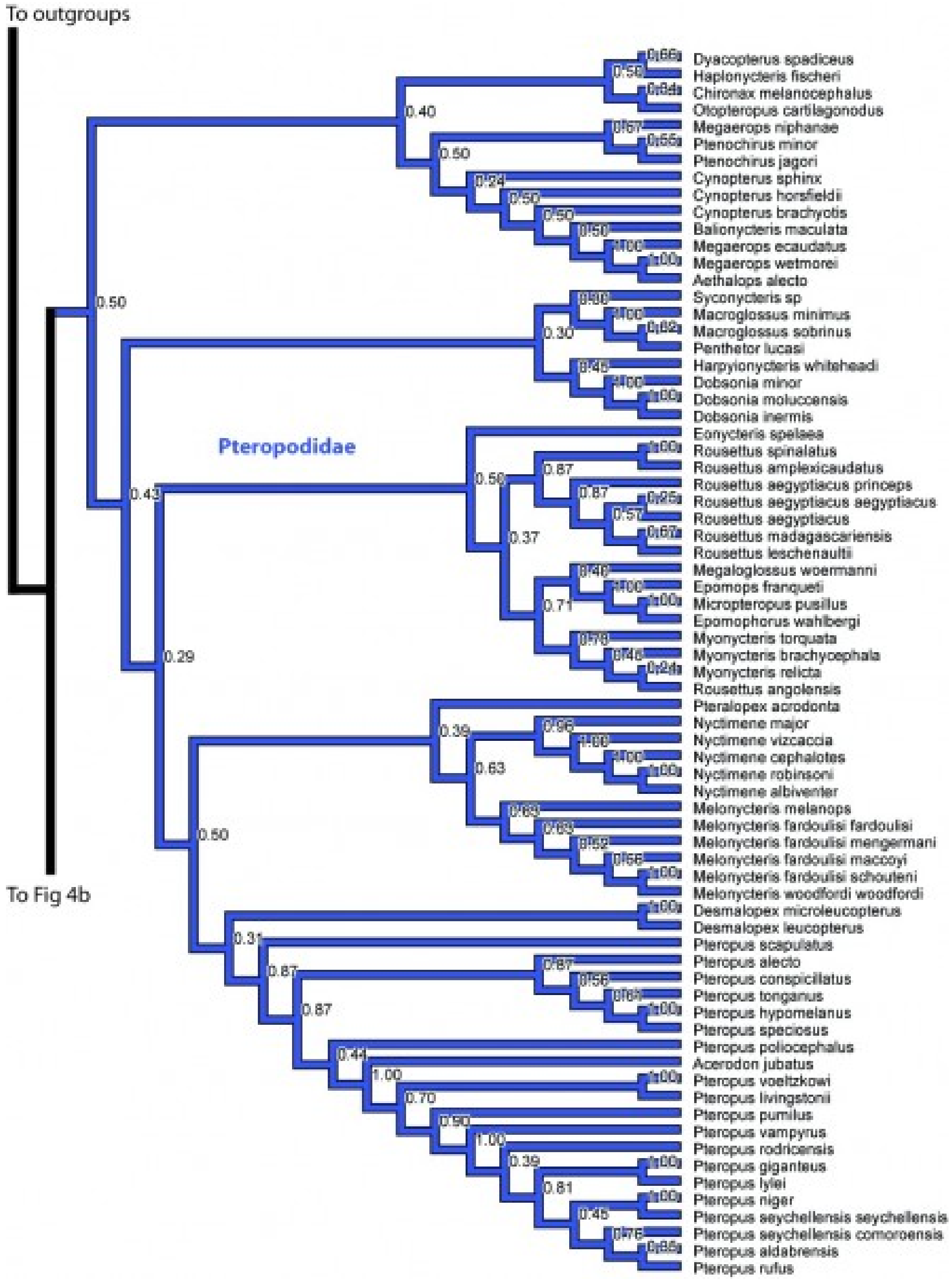

Figure 4b. Results from Figure 2, Megadermatidae, Craseonycteridae, Rhinopomatidae, Hipposideridae, and Rhinolophidae. Numbers are posterior probabilities.

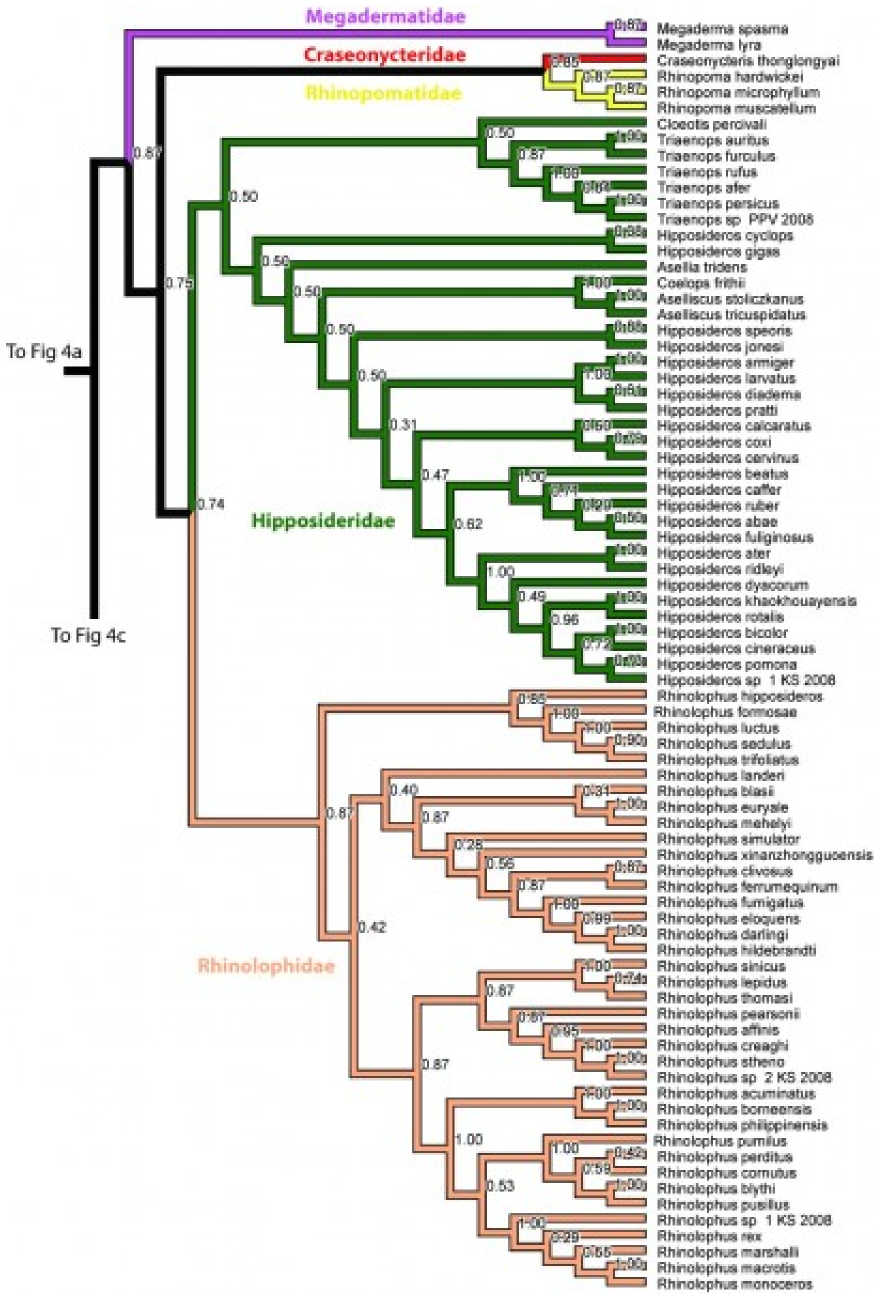

Figure 4c. Results from Figure 2, Miniopteridae, Noctilionidae, Mormoopidae, Mystacinidae, Thyropteridae, Furipteridae, and Phyllostomidae in part. Numbers are posterior probabilities.

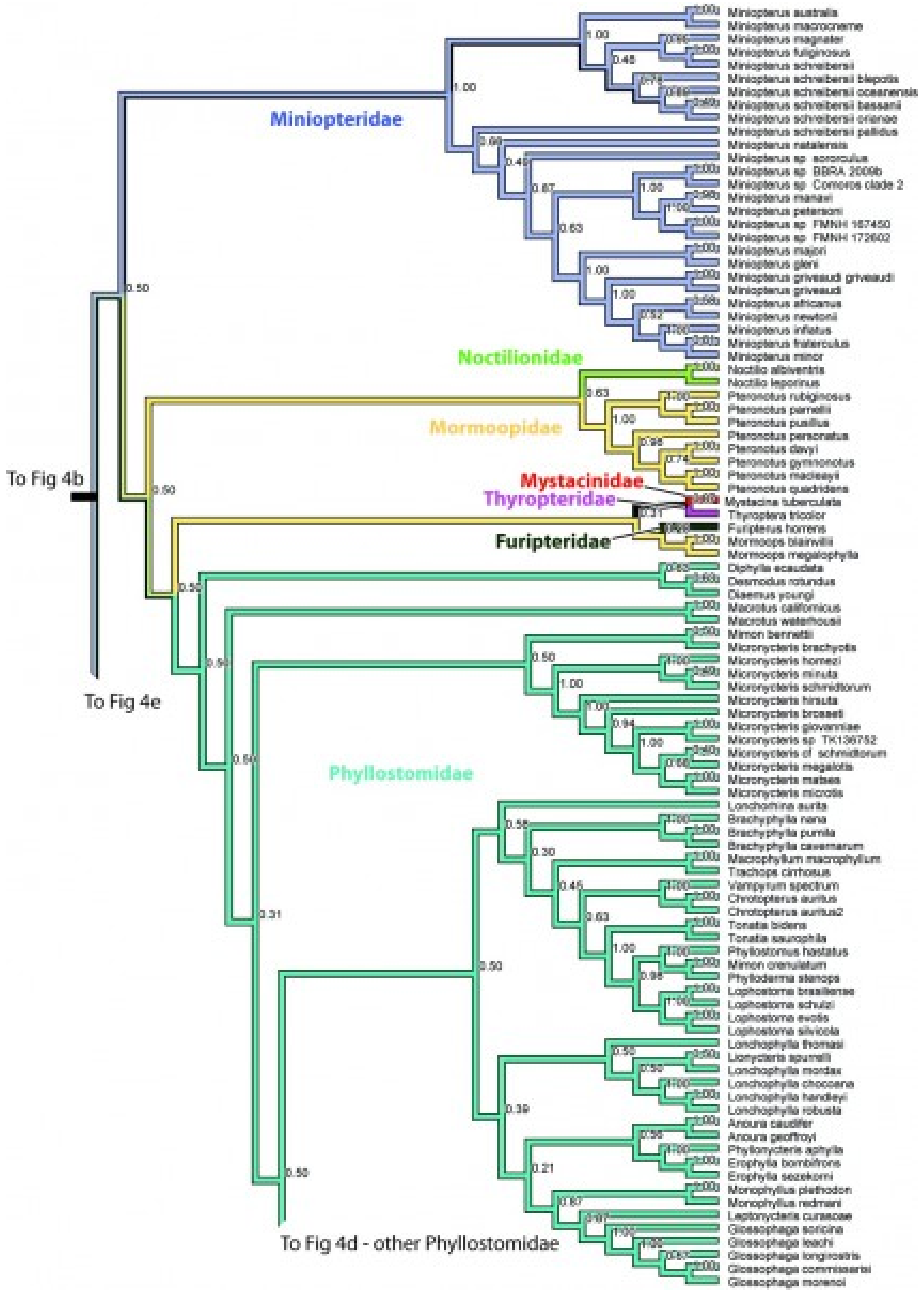

Figure 4d. Results from Figure 2, Phyllostomidae, in part. Numbers are posterior probabilities.

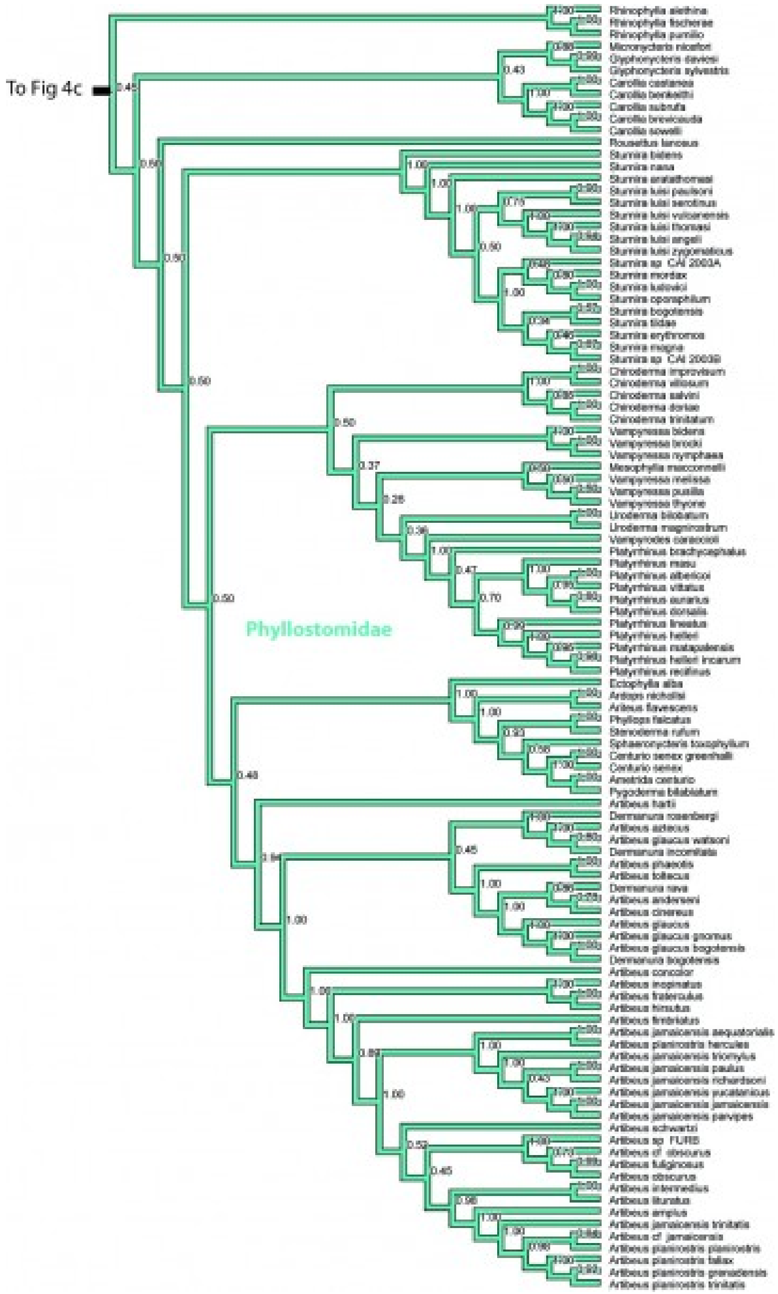

Figure 4e. Results from Figure 2, Molossidae,Emballonuridae, Myzopodidae, Natalidae, and Vespertilionidae in part. Numbers are posterior probabilities.

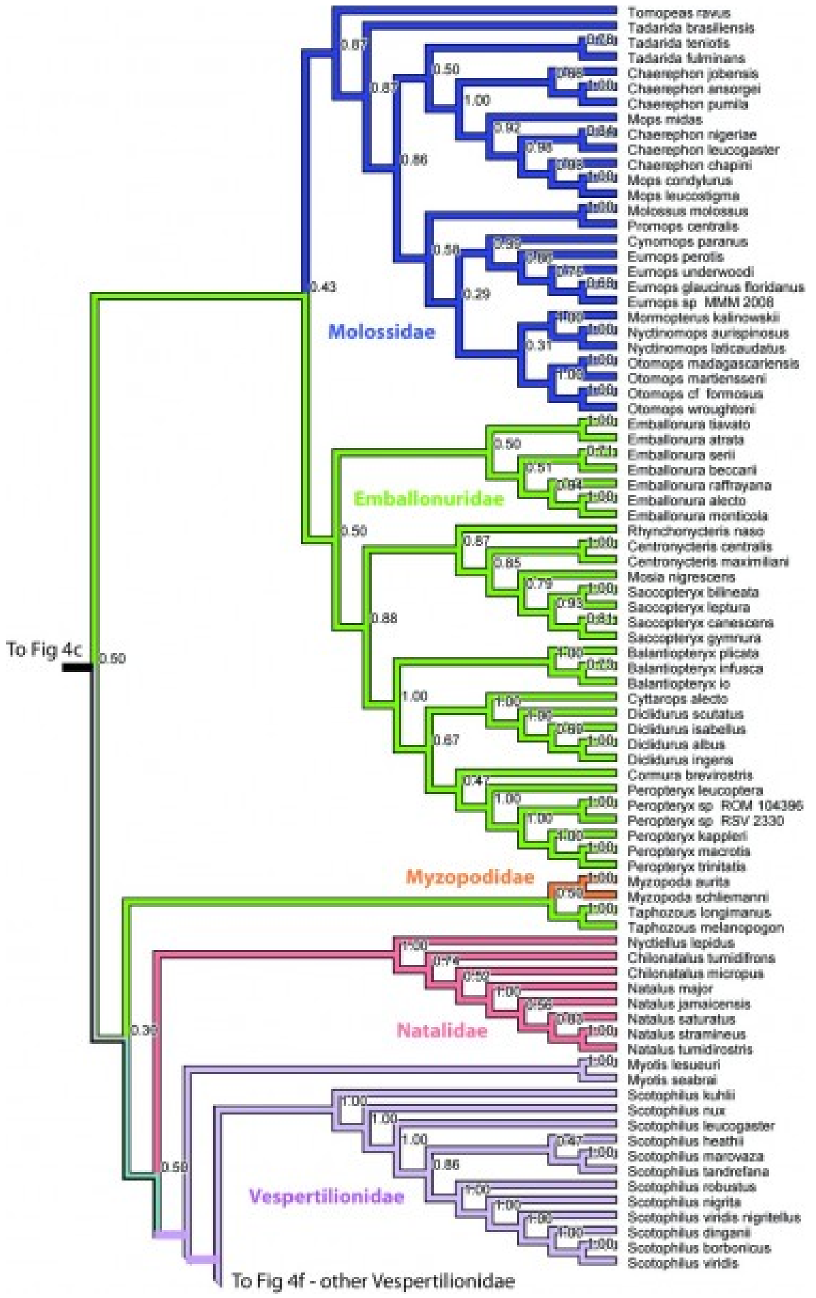

Figure 4f. Results from Figure 2, Vespertilionidae in part. Numbers are posterior probabilities.

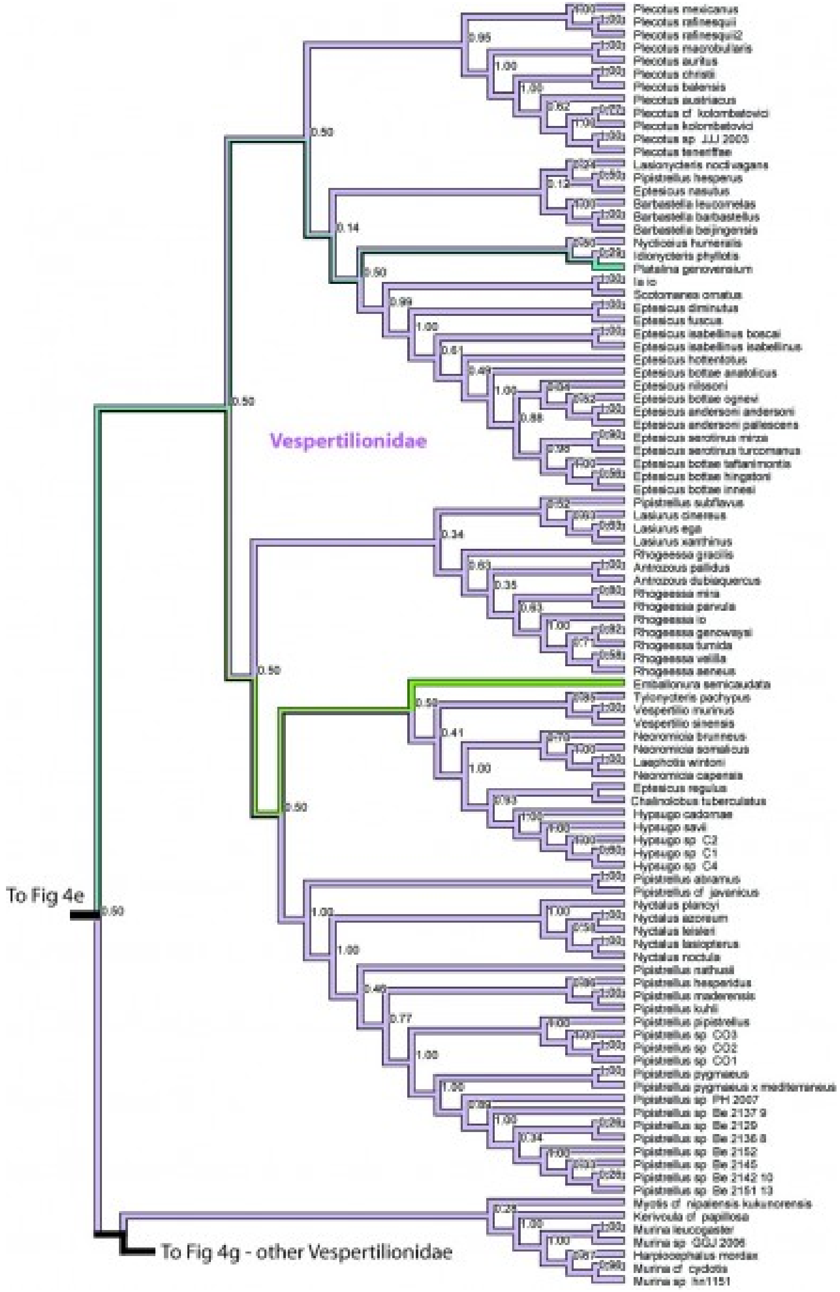

Figure 4g. Results from Figure 2, Vespertilionidae in part. Numbers are posterior probabilities.

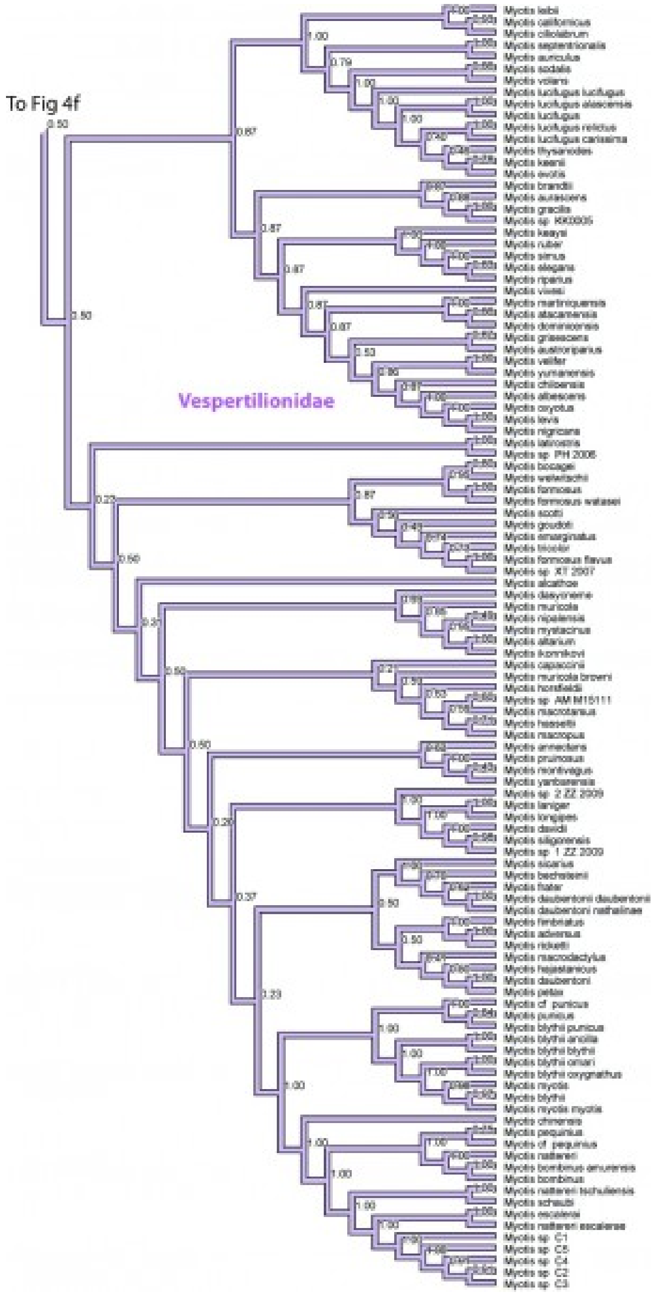

Table 1.

Species included and Genbank accession numbers

Genus	Species	sub sp or voucher	Accession Number
Acerodon	jubatus		EU330962
Aethalops	alecto		AY629006
Ametrida	centurio		AY604446
Anoura	caudifer		L19506
Anoura	geoffroyi		FJ155495
Antrozous	dubiaquercus		EF222381
Antrozous	pallidus		EF222382
Ardops	nichollsi		AY572337
Ariteus	flavescens		AY604436
Artibeus	amplus		EU160947

Artibeus	anderseni		U66509	
Artibeus	aztecus		U66510	
Artibeus	cf.jamaicensis		DQ985486	
Artibeus	cf.obscurus		DQ903818	
Artibeus	cinereus		EU805599	
Artibeus	concolor		U66519	
Artibeus	fimbriatus		U66498	
Artibeus	fraterculus		U66499	
Artibeus	fuliginosus		L19505	
Artibeus	glaucus	watsoni	FJ179259	
Artibeus	glaucus		U66512	
Artibeus	glaucus	bogotensis	EU805596	
Artibeus	glaucus	gnomus	EU805594	
Artibeus	hartii		EU160972	
Artibeus	hirsutus		U66500	
Artibeus	inopinatus		U66501	
Artibeus	intermedius		FJ179231	
Artibeus	jamaicensis	aequatorialis	DQ869450	
Artibeus	jamaicensis	jamaicensis	DQ869518	
Artibeus	jamaicensis	parvipes	DQ869474	
Artibeus	jamaicensis	paulus	DQ869456	
Artibeus	jamaicensis	richardsoni	DQ869454	
Artibeus	jamaicensis	trinitatis	DQ003028	
Artibeus	jamaicensis	triomylus	AY382782	
Artibeus	jamaicensis	yucatanicus	DQ869484	
Artibeus	lituratus		EU160813	
Artibeus	obscurus		U66507	
Artibeus	phaeotis		FJ376727	
Artibeus	planirostris	fallax	DQ869426	
Artibeus	planirostris	grenadensis	DQ869439	
Artibeus	planirostris	hercules	DQ869421	
Artibeus	planirostris	planirostris	DQ869396	
Artibeus	planirostris	trinitatis	DQ869433	
Artibeus	schwartzi		DQ869531	
Artibeus	sp.FURB		DQ985497	
Artibeus	toltecus		U66515	
Asellia	tridens		FJ457617	
Aselliscus	stoliczkanus		EU434954	
Aselliscus	tricuspidatus		DQ888679	
Balantiopterys	infusca		EF584151	
Balantiopterys	io		EF584153	
Balantiopterys	plicata		EF584154	
Balionycteris	maculata		AF044636	

Barbastella	barbastellus		EU360700
Barbastella	beijingensis		EF534762
Barbastella	leucomelas		EF534766
Brachyphylla	cavernarum		AY572383
Brachyphylla	nana		EU521680
Brachyphylla	pumila		EU521678
Carollia	benkeithi		DQ177282
Carollia	brevicauda		FJ154120
Carollia	castanea		DQ888289
Carollia	sowelli		AF511973
Carollia	subrufa		AF187024
Centronycteris	centralis		EF584155
Centronycteris	maximiliani		EF584157
Centurio	senex	greenhalli	AY604445
Centurio	senex		AY604444
Chaerephon	ansorgei		AY377967
Chaerephon	chapini		AY591329
Chaerephon	jobensis		AY591331
Chaerephon	leucogaster		EU716041
Chaerephon	nigeriae		AY591330
Chaerephon	pumila		AY614756
Chalinolobus	tuberculatus		NC_002626
Chilonatalus	micropus		AY621026
Chilonatalus	tumidifrons		AY621028
Chiroderma	improvisum		L28938
Chiroderma	doriae		AY169958
Chiroderma	salvini		L28939
Chiroderma	trinitatum		DQ312413
Chiroderma	villosum		FJ154121
Chironax	melanocephalus		AY629005
Chrotopterus	auritus		FJ155481
Cloeotis	percivali		FJ457616
Coelops	frithii		EU434955
Cormura	brevirostris		EF584159
Craseonycteris	thonglongyai		EF035012
Cynomops	paranus		AY675219
Cynopterus	brachyotis		EF201644
Cynopterus	horsfieldii		EF201643
Cynopterus	sphinx		DQ445703
Cyttarops	aleco		EF584162
Dermanura	bogotensis		FJ376714
Dermanura	rava		FJ179252
Dermanura	rosenbergi		FJ179254

Dermanura	incomitata		FJ376718
Desmalopex	leucopterus		EU330965
Desmalopex	microleucopterus		EU330976
Desmodus	rotundus		FJ155477
Diaemus	youngi		FJ155475
Diclidurus	albus		EF584163
Diclidurus	ingens		EF584164
Diclidurus	isabellus		EF584166
Diclidurus	scutatus		EF584167
Diphylla	ecaudata		FJ155476
Dobsonia	inermis		DQ445704
Dobsonia	minor		DQ445705
Dobsonia	moluccensis		AF144064
Dyacopterus	spadiceus		EF105531
Ectophylla	alba		DQ312404
Emballonura	alecto		AY426101
Emballonura	atrata		DQ178261
Emballonura	beccarrii		EF584222
Emballonura	monticola		EF584223
Emballonura	raffrayana		EF584224
Emballonura	semicaudata		EF635553
Emballonura	serii		EF635544
Emballonura	tiavato		DQ178285
Eonycteris	spelaea		AB062476
Epomophorus	wahlbergi		DQ445706
Epomops	franqueti		DQ445707
Eptesicus	andersoni	andersoni	EU786850
Eptesicus	andersoni	pallescens	EU786841
Eptesicus	bottae	anatolicus	EU786812
Eptesicus	bottae	hingstoni	EU786819
Eptesicus	bottae	innesi	EU786815
Eptesicus	bottae	ogveni	EU786876
Eptesicus	bottae	taftanimontis	EU786814
Eptesicus	diminutus		EU786864
Eptesicus	fuscus		EU786866
Eptesicus	hottentotus		EU786823
Eptesicus	isabellinus	boscai	EU786838
Eptesicus	isabellinus	isabellinus	EU786831
Eptesicus	nasutus		EU786840
Eptesicus	nilssoni		AF376836
Eptesicus	regulus		AY007531
Eptesicus	serotinus	mirza	EU786861
Eptesicus	serotinus	turcomanus	EU786875

Erophylla	bombifrons		AY620438
Erophylla	sezekorni		AY620439
Eumops	glaucinus	floridanus	EU350026
Eumops	perotis		EU349991
Eumops	sp.	MMM-2008	EU349999
Eumops	underwoodi		EU349989
Furipterus	horrens		AY621004
Glossophaga	commissarisi		AF382886
Glossophaga	leachi		AF382878
Glossophaga	longirostris		AF382875
Glossophaga	morenoi		AF382882
Glossophaga	soricina		FJ392516
Glyphonycteris	daviesi		AY380747
Glyphonycteris	sylvestris		AY380746
Haplonycteris	fischeri		AY817881
Harpiocephalus	mordax		AJ841971
Harpyionycteris	whiteheadi		DQ445708
Hipposideros	abae		EU934448
Hipposideros	armiger		EU434946
Hipposideros	ater		DQ054807
Hipposideros	beatus		FJ347976
Hipposideros	bicolor		DQ054808
Hipposideros	caffer		FJ347980
Hipposideros	calcaratus		DQ054806
Hipposideros	cervinus		DQ054805
Hipposideros	cineraceus		DQ054809
Hipposideros	coxi		EF108148
Hipposideros	cyclops		EU934466
Hipposideros	diadema		DQ219421
Hipposideros	dyacorum		EF108151
Hipposideros	fuliginosus		EU934468
Hipposideros	gigas		EU934470
Hipposideros	jonesi		EU934473
Hipposideros	khaokhouayensis		DQ054816
Hipposideros	larvatus		EU434949
Hipposideros	pomona		EU434950
Hipposideros	pratti		EU434952
Hipposideros	ridleyi		DQ054812
Hipposideros	rotalis		DQ054814
Hipposideros	ruber		FJ347996
Hipposideros	sp.1KS-2008		EU434948
Hipposideros	speoris		DQ680823

Hypsugo	cardonae		DQ318883
Hypsugo	savii		DQ120866
Hypsugo	sp.C1		EU360677
Hypsugo	sp.C2		EU360678
Hypsugo	sp.C4		EU360679
Ia	io		DQ302094
Idionycteris	phyllotis		IINMTCYTB
Kerivoula	cf.papillosa		AJ841970
Laephotis	wintoni		AJ841964
Lasionycteris	noctivagans		LSNMTCYTBZ
Lasiurus	cinereus		DQ421825
Lasiurus	ega		DQ421826
Lasiurus	xanthinus		AF369549
Leptonycteris	curasoae		AF382889
Lionycteris	spurrelli		AF423100
Lonchophylla	chocoana		AF423092
Lonchophylla	handleyi		AF423094
Lonchophylla	mordax		AF423095
Lonchophylla	robusta		AF423091
Lonchophylla	thomasi		AF423086
Lonchorhina	aurita		FJ155494
Lophostoma	silvicola		FJ155493
Lophostoma	brasiliense		FJ155486
Lophostoma	evotis		FJ155491
Lophostoma	schulzi		FJ155485
Macroglossus	minimus		AY926645
Macroglossus	sobrinus		FJ226494
Macrophyllum	macrophyllum		FJ155484
Macrotus	californicus		AY380744
Macrotus	waterhousii		AY380745
Megaderma	lyra		DQ888678
Megaderma	spasma		AY057942
Megaerops	ecaudatus		EF201645
Megaerops	niphanae		AF044647
Megaerops	wetmorei		EF105537
Megaloglossus	woermanni		DQ445710
Melonycteris	fardoulisi	fardoulisi	AY847251
Melonycteris	fardoulisi	maccoyi	AY847254
Melonycteris	fardoulisi	mengermani	AY847241
Melonycteris	fardoulisi	schouteni	AY847236
Melonycteris	melanops		AF044645
Melonycteris	woodfordi	woodfordi	AY847234
Mesophylla	macconnelli		FJ154122

Micronycteris	brachyotis		AY380748
Micronycteris	brosseti		AY380771
Micronycteris	cf.schmidtorum		DQ077407
Micronycteris	giovanniae		AY380750
Micronycteris	hirsuta		DQ077415
Micronycteris	homezi		AY380754
Micronycteris	matses		DQ077419
Micronycteris	megalotis		DQ077429
Micronycteris	microtis		AY380756
Micronycteris	minuta		DQ077405
Micronycteris	schmidtorum		DQ077442
Micronycteris	sp.TK136752		DQ077420
Micronycteris	nicefori		AY380749
Micropteropus	pusillus		AF044648
Mimon	crenulatum		FJ155478
Mimon	bennettii		DQ903832
Miniopterus	africanus		EF363524
Miniopterus	australis		AY614735
Miniopterus	fraterculus		AJ841975
Miniopterus	fuliginosus		AB085735
Miniopterus	gleni		FJ383146
Miniopterus	griveaudi		FJ232802
Miniopterus	griveaudi	griveaudi	FJ383143
Miniopterus	inflatus		AY614737
Miniopterus	macrocneme		AY614734
Miniopterus	magnater		EF517308
Miniopterus	majori		DQ899776
Miniopterus	manavi		FJ383130
Miniopterus	minor		FJ232805
Miniopterus	natalensis		AY614744
Miniopterus	newtonii		EF363521
Miniopterus	petersoni		EU091258
Miniopterus	pusillus		DQ837650
Miniopterus	schreibersii		EF530348
Miniopterus	schreibersii	bassanii	AY614733
Miniopterus	schreibersii	blepotis	AF217444
Miniopterus	schreibersii	oceanensis	AF130123
Miniopterus	schreibersii	orianae	AY614732
Miniopterus	schreibersii	pallidus	AY614736
Miniopterus	sp.	BBRA-2009b	FJ383134
Miniopterus	sp.	Comoros clade 2	FJ232800
Miniopterus	sp.	FMNH 167450	FJ383132
Miniopterus	sp.	FMNH 172602	FJ383133

Miniopterus	sp.	sororculus	DQ899771
Molossus	molossus		L19724
Monophyllus	plethodon		AF382887
Monophyllus	redmani		AF382888
Mops	condylurus		EF474030
Mops	leucostigma		EF474029
Mops	midas		EF474049
Mormoops	blainvillii		AY604462
Mormoops	megalophylla		AF330808
Mormopterus	kalinowskii		L19725
Mosia	nigrescens		EF635558
Murina	cf.cyclotis		AJ841974
Murina	leucogaster		AB085733
Murina	sp.	GGJ-2006	DQ435071
Murina	sp.	hn1151	EF570883
Myonycteris	brachycephala		AF044644
Myonycteris	relicta		AF044649
Myonycteris	torquata		AF044650
Myotis	adversus		AB106587
Myotis	albescens		AF376839
Myotis	alcathoe		AJ841955
Myotis	altarium		FJ215677
Myotis	annectans		AJ841956
Myotis	atacamensis		AM261882
Myotis	aurascens		AY665161
Myotis	auriculus		AM261884
Myotis	austroripari		AM261885
Myotis	bechsteinii		AF376843
Myotis	blythii		DQ120906
Myotis	blythii	ancilla	AM284170
Myotis	blythii	blythii	AF376840
Myotis	blythii	omari	DQ288853
Myotis	blythii	oxygnathus	AF376841
Myotis	blythii	punicus	AF376842
Myotis	bocagei		AJ504408
Myotis	bombinus		EF555240
Myotis	bombinus	amurensis	AM284169
Myotis	brandtii		AM261886
Myotis	californicus		AM261887
Myotis	capaccinii		AF376845
Myotis	cf.nipalensis	kukunorensis	AY699845
Myotis	cf.pequinius		AM284173
Myotis	cf.punicus		AF246252

Myotis	chiloensis		AM261888
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Myotis	ciliolabrum		AM261889
Myotis	dasycneme		AF376846
Myotis	daubentoni		AY665137
Myotis	daubentoni	nathalinae	AF376862
Myotis	daubentoni	daubentonii	EU153105
Myotis	davidii		AB106591
Myotis	dominicensis		AF376848
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Myotis	formosus	flavus	EU434932
Myotis	formosus	watasei	EU434933
Myotis	frater		AB106593
Myotis	goudoti		AJ504451
Myotis	gracilis		AB243029
Myotis	grisescens		AM261892
Myotis	hajastanicus		AY665138
Myotis	hasseltii		AF376850
Myotis	horsfieldii		AF376851
Myotis	ikonnikovi		AB106602
Myotis	keaysi		AF376852
Myotis	keenii		AM262329
Myotis	laniger		EF555229
Myotis	latirostris		AM262330
Myotis	leibii		AM262331
Myotis	lesueuri		AY485687
Myotis	levis		AF376853
Myotis	longipes		FJ215678
Myotis	lucifugus		AF376854
Myotis	lucifugus	alascensis	DQ503483
Myotis	lucifugus	carissima	AF294512
Myotis	lucifugus	lucifugus	DQ503488
Myotis	lucifugus	relictus	DQ503558
Myotis	macrodactylus		EF555238
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Myotis	macrotarsus		AJ841960
Myotis	martiniquensis		AM262332

Myotis	montivagus		AM262333
Myotis	muricola		AY665144
Myotis	muricola	browni	AF376859
Myotis	myotis		AM261883
Myotis	myotis	myotis	AF246246
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Myotis	nattereri		AB106606
Myotis	nattereri	escalerae	EU360649
Myotis	nattereri	tschuliensis	AM284171
Myotis	nigricans		AF376864
Myotis	nipalensis		AY699844
Myotis	oxyotus		AF376865
Myotis	pequinius		AM284172
Myotis	petax		EF555236
Myotis	pruinosus		AB106607
Myotis	punicus		EU360640
Myotis	ricketti		AJ504452
Myotis	riparius		AF376866
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Myotis	seabrai		AJ841962
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Myotis	sicarius		AJ841951
Myotis	siligorensis		FJ215679
Myotis	simus		AM262336
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Myotis	tricolor		AJ841952
Myotis	velifer		AF376870
Myotis	vivesi		AJ504406
Myotis	volans		AF376871

Myotis	welwitschii		AF376874
Myotis	yanbarensis		AB106610
Myotis	yumanensis		AF376875
Mystacina	tuberculata		AY960981
Myzopoda	aurita		EF432190
Myzopoda	schliemanni		EF432213
Natalus	jamaicensis		AY621023
Natalus	major		AY621021
Natalus	saturatus		AY621014
Natalus	stramineus		AY621019
Natalus	tumidirostris		AY621008
Neoromicia	brunneus		EU786868
Neoromicia	capensis		AJ841966
Neoromicia	somalicus		EU786869
Noctilio	albiventris		AF330806
Nyctalus	azoreum		DQ887590
Nyctalus	lasiopterus		DQ120871
Nyctalus	leisleri		AF376832
Nyctalus	noctula		AJ841967
Nyctalus	plancyi		DQ435073
Nycteris	leporinus		AF330802
Nycticeius	humeralis		L19727
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Nyctimene	albiventer		DQ314264
Nyctimene	cephalotes		DQ314268
Nyctimene	major		AF044652
Nyctimene	robinsoni		AF144066
Nyctimene	vizcaccia		DQ445711
Nyctinomops	aurispinosus		L19728
Nyctinomops	laticaudatus		L19729
Otomops	cf.formosus		EF504252
Otomops	madagascariensis		EF216381
Otomops	martiensseni		EF216441
Otomops	wroughtoni		EF504251
Otopteropus	cartilagonodus		AY974770
Penthetor	lucasi		EF105542
Peropteryx	kappleri		EF584169
Peropteryx	leucoptera		EF584175
Peropteryx	macrotis		EF584180
Peropteryx	spvoucherROM104396		EF584170
Peropteryx	spvoucherRSV2330		EF584171
Peropteryx	trinitatis		EF584182
Phylloderma	stenops		FJ155480

Phyllonycteris	aphylla		AF187033
Phyllops	falcatus		DQ211651
Phyllostomus	hastatus		FJ155479
Pipistrellus	abramus		AJ504448
Pipistrellus	cf.javanicus		AJ504447
Pipistrellus	hesperidus		AJ841968
Pipistrellus	hesperus		DQ421823
Pipistrellus	kuhli		AJ504444
Pipistrellus	maderensis		AJ426632
Pipistrellus	nathusii		AJ504446
Pipistrellus	pipistrellus		AJ504443
Pipistrellus	pygmaeus		DQ120856
Pipistrellus	pygmaeusxmediterraneus	AJ504442	
Pipistrellus	sp.	Be_2136_8	AY426091
Pipistrellus	sp.	Be_2137_9	AY426092
Pipistrellus	sp.	Be_2142_10	AY426089
Pipistrellus	sp.	Be_2145	AY316334
Pipistrellus	sp.	Be_2151_13	AY426090
Pipistrellus	sp.	Be_2152	AY316332
Pipistrellus	sp.	CO1	EU420890
Pipistrellus	sp.	CO2	EU420891
Pipistrellus	sp.	CO3	EU420892
Pipistrellus	sp.	PH-2007	EF370417
Pipistrellus	sp.	Be_2129	AY316333
Pipistrellus	subflavus		AJ504449
Platalina	genovensium		AF423101
Platyrrhinus	albericoi		FJ154124
Platyrrhinus	helleri		FJ154141
Platyrrhinus	helleri	incarum	FJ154146
Platyrrhinus	masu		FJ154164
Platyrrhinus	matapalensis		FJ154168
Platyrrhinus	aurarius		FJ154127
Platyrrhinus	brachycephalus		FJ154132
Platyrrhinus	dorsalis		FJ154139
Platyrrhinus	lineatus		FJ154160
Platyrrhinus	recifinus		FJ154176
Platyrrhinus	vittatus		FJ154178
Plecotus	auritus		EF570882
Plecotus	austriacus		EU360707
Plecotus	balensis		AF513798
Plecotus	cf.kolombatovici		AF513783
Plecotus	christii		EU743801
Plecotus	kolombatovici		AF513785

Plecotus	macrobullaris		AF513805
Plecotus	mexicanus		AY776038
Plecotus	rafinesquii		AY776084
Plecotus	sp.	JJJ-2003	AF513791
Plecotus	teneriffae		EU360704
Promops	centralis		L19732
Ptenochirus	jagori		AB046325
Ptenochirus	minor		AY974702
Pteralopex	acrodonta		FJ561376
Pteronotus	davyi		AF338672
Pteronotus	gymnonotus		AF338675
Pteronotus	macleayii		AY604461
Pteronotus	parnellii		AY604456
Pteronotus	personatus		AF338680
Pteronotus	pusillus		AY604455
Pteronotus	quadridens		AY604460
Pteronotus	rubiginosus		AY604457
Pteropus	rufus		AB085732
Pteropus	aldabrensis		FJ561394
Pteropus	alecto		AF144065
Pteropus	conspicillatus		FJ561380
Pteropus	giganteus		FJ561381
Pteropus	hypomelanus		FJ561383
Pteropus	livingstonii		FJ561384
Pteropus	lylei		EF584229
Pteropus	niger		FJ561385
Pteropus	poliocephalus		FJ561387
Pteropus	pumilus		FJ561390
Pteropus	rodricensis		FJ561392
Pteropus	scapulatus		FJ561377
Pteropus	seychellensis	seychellensis	FJ561399
Pteropus	seychellensis	comoroensis	FJ561398
Pteropus	speciosus		AB062474
Pteropus	tonganus		AF044656
Pteropus	vampyrus		FJ561401
Pteropus	voeltzkowi		FJ561405
Pygoderma	bilabiatum		AY604438
Rhinolophus	acumiatus		EF108155
Rhinolophus	affinis		EU434934
Rhinolophus	blasii		EU436669
Rhinolophus	blythi		DQ865344
Rhinolophus	borneensis		EF108162
Rhinolophus	clivosus		EU436674

Rhinolophus	cornutus		DQ297594
Rhinolophus	creaghi		EF108164
Rhinolophus	darlingi		EU436675
Rhinolophus	eloquens		EU436677
Rhinolophus	eurvale		EU436671
Rhinolophus	ferrumequinum		EU436673
Rhinolophus	formosae		NC_011304
Rhinolophus	fumigatus		EU436678
Rhinolophus	hildebrandti		EU436676
Rhinolophus	hipposideros		EU360631
Rhinolophus	landeri		FJ457612
Rhinolophus	lepidus		AF451338
Rhinolophus	luctus		EF544422
Rhinolophus	macrotis		EU434957
Rhinolophus	marshalli		EU434938
Rhinolophus	mehelyi		EU436672
Rhinolophus	monocerus		EF555788
Rhinolophus	pearsonii		EU434940
Rhinolophus	perditus		AY141039
Rhinolophus	philippinensis		EF108169
Rhinolophus	pumilus		NC_005434
Rhinolophus	pusillus		EF217392
Rhinolophus	rex		EU075216
Rhinolophus	sedulus		EF108174
Rhinolophus	simulator		EU436670
Rhinolophus	sinicus		EU434941
Rhinolophus	sp.1KS-2008		EU434937
Rhinolophus	sp.2KS-2008		EU434942
Rhinolophus	stheno		EF108175
Rhinolophus	thomasi		EU434943
Rhinolophus	trifoliatus		EF108177
Rhinolophus	xinanzhongguoensis		EU750753
Rhinophylla	alethina		AF187028
Rhinophylla	fischerae		AF187032
Rhinophylla	pumilio		AF187031
Rhinopoma	hardwickei		AY056462
Rhinopoma	microphyllum		AM931063
Rhinopoma	muscatellum		DQ337500
Rhogeessa	aeneus		EF222359
Rhogeessa	genowaysi		EF222326
Rhogeessa	gracilis		EF222412
Rhogeessa	io		EF222392

Rhogeessa	mira		EF222336
Rhogeessa	parvula		EF222355
Rhogeessa	tumida		EF222367
Rhogeessa	velilla		EF222341
Rhynchonycteris	naso		EF584192
Rousettus	aegyptiacus		EU624124
Rousettus	aegyptiacus	aegyptiacus	AF044658
Rousettus	aegyptiacus	princeps	AF044659
Rousettus	amplexicaudatus		AB046329
Rousettus	angolensis		AF044643
Rousettus	lanosus		AF044661
Rousettus	leschenaultii		FJ549331
Rousettus	madagascariensis		AF044663
Rousettus	spinalatus		EF105523
Saccopterix	bilineata		EF584202
Saccopterix	canescens		EF584206
Saccopterix	gymnura		EF584208
Saccopterix	leptura		EF584216
Scotomanes	ornatus		DQ435069
Scotophilus	borbonicus		DQ459067
Scotophilus	dinganii		EU750999
Scotophilus	heathii		EU750946
Scotophilus	kuhlii		EU750931
Scotophilus	leucogaster		EU750940
Scotophilus	marovaza		EU750943
Scotophilus	nigrita		EU750955
Scotophilus	nux		EU750939
Scotophilus	robustus		EU750948
Scotophilus	tandrefana		EU750941
Scotophilus	viridis		EU750991
Scotophilus	viridis	nigritellus	EU750976
Sphaeronycteris	toxophyllum		AY604452
Stenoderma	rufum		AY604431
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Sturnira	luisi	thomasi	AF435250
Sturnira	luisi	vulcanensis	AF435251
Sturnira	aratathomasi		AF435252
Sturnira	bidens		AF435201
Sturnira	bogotensis		AF435248
Sturnira	erythromos		FJ154179
Sturnira	ludovici		AF435235
Sturnira	luisi	angeli	AF435158
Sturnira	luisi	paulsoni	AF435162

Sturnira	luisi	zygomaticus	AF435159
Sturnira	magna		AF435180
Sturnira	mordax		AF435212
Sturnira	nana		AF435253
Sturnira	oporaphilum		AF435210
Sturnira	sp.CAI-2003A		AF435203
Sturnira	sp.CAI-2003B		AF435204
Sturnira	lilium		AF187035
Sturnira	tildae		AF435185
Syconycteris	sp.		AF044665
Tadarida	brasiliensis		L19734
Tadarida	fulminans		EU760911
Tadarida	teniotis		EU360721
Taphozous	longimanes		EF584219
Taphozous	melanopogon		EF584221
Thyroptera	tricolor		AY621005
Tomopeas	ravus		L19735
Tonatia	bidens		FJ155490
Tonatia	saurophila		FJ155488
Trachops	cirrhosus		FJ155483
Triaenops	afer		EU798750
Triaenops	auritus		DQ005794
Triaenops	furculus		DQ005845
Triaenops	persicus		EU798758
Triaenops	rufus		DQ005771
Triaenops	sp.PPV-2008		EU798756
Tylonycteris	pachypus		EF517315
Uroderma	bilobatum		AY169955
Uroderma	magnirostrum		FJ154180
Vampyressa	bidens		AY157055
Vampyressa	melissa		FJ154185
Vampyressa	pusilla		DQ312428
Vampyressa	thyone		DQ312431
Vampyressa	brocki		DQ312421
Vampyressa	nymphaea		DQ312418
Vampyrodes	caraccioli		FJ154184
Vampyrum	spectrum		FJ155482
Vespertilio	murinus		AB287359
Vespertilio	sinensis		AB287362

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