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BATS, CLOCKS, AND ROCKS: DIVERSIFICATION PATTERNS IN CHIROPTERA

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Abstract.—Identifying nonrandom clade diversification is a critical first step toward understanding the evolutionary processes underlying any radiation and how best to preserve future phylogenetic diversity. However, differences in diversification rates have not been quantitatively assessed for the majority of groups because of the lack of necessary analytical tools (e.g., complete species-level phylogenies, estimates of divergence times, and robust statistics which incorporate phylogenetic uncertainty and test appropriate null models of clade growth). Here, for the first time, we investigate diversification rate heterogeneity in one of the largest groups studied thus far, the bats (Mammalia: Chiroptera). We use a recent, robust statistical approach (whole-tree likelihood-based relative rate tests) on complete dated species-level supertree phylogenies. As has been demonstrated previously for most other groups, among-lineage diversification rate within bats has not been constant. However, we show that bat diversification is more heterogeneous than in other mammalian clades thus far studied. The whole-tree likelihood-based relative rates tests suggest that clades within the families Phyllostomidae and Molossidae underwent a number of significant changes in relative diversification rate. There is also some evidence for rate shifts within Pteropodidae, Emballonuridae, Rhinolophidae, Hipposideridae, and Vespertilionidae, but the significance of these shifts depends on polytomy resolution within each family. Diversification rate in bats has also not been constant, with the largest diversification rate shifts occurring 30–50 million years ago, a time overlapping with the greatest number of shifts in flowering plant diversification rates.

Key words.—Bats, clade growth models, diversification rates, fossils, molecular sequences, phylogeny.

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One may hypothesize that bats did originate, but it is harder to go beyond this. Van Valen (1979, p. 103)

As Van Valen suggested, investigating evolutionary patterns in bats is a challenge: bats have a poor fossil record (Hand 1984), their phylogenetic relationships are little studied (reviewed in Jones et al. 2002), and many examples of cryptic speciation are known (e.g., Mayer and von Helversen 2001) making even species recognition difficult. It is unsurprising then that bat diversification patterns have never been examined in a quantitative manner, despite the fact that bats comprise about one-fifth of all mammals, are one of the most ecologically and morphologically diverse mammalian clades, have adapted to almost every terrestrial environment on the planet, and play important roles in ecosystem functioning (Simmons and Conway 2003). The heterogeneous taxonomic distribution of species diversity among bat families does suggest that clades have differed with respect to their past speciation and extinction probabilities, with many species-poor (e.g., families Craseonycteridae, Furipteridae, Mystacinidae, Myzopodidae, and Thyropteridae) and a few species-rich clades (e.g., Vespertilionidae, Phyllostomidae, Pteropodidae, and Rhinolophidae) (Koopman 1993).

Recently, there has been a resurgence of interest in and studies of bat phylogenetic relationships (e.g., Springer et al. 2001; Teeling et al. 2003, 2005). Additionally bat alpha taxonomy has greatly improved (Simmons 2006) and new methods for studying evolutionary diversification have been developed that do not rely on fossils, but instead use the distribution of species diversity among extant taxa in a phylogeny (reviewed in Mooers and Heard 1997; Barraclough and Nee 2001; Moore et al. 2004). Thus, a more rigorous and quantitative assessment of bat diversification patterns is now possible for the first time.

Identifying nonrandom differences in clade diversification is a critical first step towards understanding the evolutionary processes responsible for such patterns (Moore et al. 2004) and how best to preserve future phylogenetic diversity (Mace et al. 2003). Temporal diversification statistical methods use the timing of speciation events in a phylogeny and compare the observed distribution of speciation events through time with that expected under a null model of cladogensis (e.g., Paradis 1997; Nee 2001). By contrast, topological diversification statistics use only the topology of the phylogeny to compare species diversity at each node to that expected under a random model (i.e., because sister-taxa are the same age, they are expected to contain the same number of descendant taxa). Examples of topology-based statistics include those that assess the significance of imbalances at single nodes within the phylogeny (e.g., Slowinski and Guyer 1993), and those that summarize tree symmetry as a single number across all the nodes in the phylogeny (e.g., Colless 1982; Shao and Sokal 1990). These temporal and topological diversification statistics often require resolved and complete species-level phylogenies (plus estimates of divergence times for the temporal statistics), all of which are lacking for many groups (Bininda-Emonds 2004a). It is unsurprising then that differences in diversification rates have not been quantitatively assessed for the majority of groups. However, interesting patterns are emerging from the relatively few studies conducted to date. For example, most phylogenies seem to be much more imbalanced than expected from null models of clade growth (e.g., Purvis and Agapow 2002; Sims and McConway 2003) and a number of ecological and environmental factors have recently been demonstrated to correlate

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with diversification rate heterogeneity among and within clades, including climbing ability in flowering plants (Gianoli 2004), morphological adaptations of flowers to specialist pollinators (Sargent 2004), environmental energy available to flowering plants (Davies et al. 2004a), morphological diversity in passerine birds (Ricklefs 2004), and life history and ecology in mammals (Isaac et al. 2005).

With the development of supertree construction methodologies (reviewed in Bininda-Emonds 2004a,b) and improved phylogenetic dating techniques in the absence of molecular clocks (e.g., Sanderson 2002; Rannala and Yang 2003), there has been an increase in the number of both complete species-level phylogenies and trees containing estimates of divergence times. Additionally, diversification statistics have also improved (e.g., McConway and Sims 2004; Moore et al. 2004), incorporating more appropriate null models of clade growth and phylogenetic uncertainty (e.g., different topologies and unresolved nodes) into analyses (e.g., Chan and Moore 2005).

Here, for the first time, we employ a range of diversification statistics, a complete species-level bat supertree (Jones et al. 2002) and the timing of these divergence events (which we calculate here for the first time) to investigate three questions about bat diversification: (1) Is the rate of diversification constant over all lineages? (2) Which lineages are responsible for any shifts in diversification rate? (3) Are any changes in diversification concentrated at particular time intervals? The power of our approach is that we avoid errors due to incomplete or nonrandom taxonomic sampling by using complete species-level phylogenies, incorporate phylogenetic uncertainty (due to different topologies and unresolved nodes), and employ a range of diversification statistics and null models to identify consistent diversification patterns.

Materials and Methods

Phylogenetic Information

Our investigations into the patterns in diversification are based on our existing species-level supertree of all extant bat species (Jones et al. 2002). Recent molecular phylogenetic studies have suggested a fundamental rearrangement of higher-level relationships (e.g., Teeling et al. 2003; 2005), with the suborder Megachiroptera nesting within the suborder Microchiroptera, to render the latter paraphyletic. We therefore generated an alternative supertree with the family-level topology rearranged according to a recent complete family-level molecular tree (Teeling et al. 2005) and performed all analyses on both phylogenies.

We also required divergence time estimates in these phylogenies for the temporal analyses of diversification patterns (see below). Divergence times are commonly estimated by transforming the relative amount of molecular sequence divergence among taxa into estimates of time. Assuming that nucleotide substitutions between taxa accumulate randomly over time, the molecular distances of speciation events in phylogenies are expected to be roughly proportional to the time elapsed (the molecular clock hypothesis). Sequence divergence rates can then be calibrated to absolute dates derived from fossils. Recently, this area has rapidly improved with methods that account for the often nonclock behavior of nucleotide substitutions and variation in substitution rates among lineages, including nonparametric rate smoothing (Sanderson 1997), penalized likelihood (Sanderson 2002), or various Bayesian methods (e.g., Thorne and Kishino 2002; Rannala and Yang 2003).

Unfortunately, the computational complexity of these methods generally prohibits their use on phylogenies containing large numbers of taxa. Perhaps more importantly, the distribution of molecular sequence data for bats is extremely patchy, such that no single gene has been sampled for all species in the clade. As such, the methods listed above would have to contend with an extremely large amount of missing data and poor overlap, both of which would have deleterious effects.

Therefore, to estimate divergence times in the bat supertree phylogenies (916 species), we extend a methodology (Purvis 1995; Bininda-Emonds et al. 1999) that can be applied to extremely large clades and that does not assume sequence divergence is clocklike. Our method, like other approaches, fits molecular sequences to given topologies, but then determines the ages of all nodes in that topology relative to an ancestral one (i.e., node x is x% as old as its ancestral node y). These relative divergences are then calibrated from either fossil information or absolute molecular dates. Although the fossil and absolute molecular dates act as the ultimate calibration points for the relative molecular nodal date estimate, the calibrated relative molecular dates for a given node can also be used to calibrate the relative molecular divergences of nodes descending from it. Thus, the date for any particular node may come from fossil dates, absolute molecular dates, and/or from dates that have been generated from calibrated relative sequence divergences of different genes.

In contrast to the dating method developed by Vos and Mooers (2004), our approach does not require that the genes evolve according to a strict molecular clock. Instead, only a local molecular clock is assumed (Purvis 1995) because the evolutionary rate is only held to be similar between the branches contributing to any relative molecular date. Our method allows the retention of a far greater amount of molecular data than the method of Vos and Mooers (2004), which requires sequences to be deleted to satisfy the assumption of a strict clock. Additionally, our method improves upon that used to date other supertrees (primates: Purvis 1995; carnivores: Bininda-Emonds et al. 1999) because the divergence information is directly fitted onto the topology rather than being indirectly mapped onto the supertree from published molecular phylogenies. This avoids the issue of incongruence between the source and the supertree, incorrect assumptions of the behavior of molecular substitution rates within and among lineages, and data duplication where data from the same gene are used to calculate distances for the same taxa. Detailed information of our method follows.

Data were gathered for the 429 nodes in the original supertree (431 nodes in the alternative topology) in four ways: (1) relative molecular dates (original: 402 date estimates for 178 nodes, alternative: 420 for 182); (2) fossil dates (647 date estimates for 98 nodes, alternative: 104 nodes); (3) absolute molecular dates (eight date estimates for one node for both topologies); and (4) interpolated dates (one date estimate

TABLE 1. Summary statistics for the six gene sequences downloaded from GenBank. Lengths in parentheses for 12S and 16S rDNA represent the actual number of base pairs that were analyzed after regions that could not be aligned unambiguously were excluded. The optimal model of evolution was determined using ModelTest version 3.06 (Posada and Crandall 1998); for a description of the models, see Posada and Crandall (1998).

Gene	No. of specimens	No. of species	Aligned length (bp)	Optimal model of evolution
12S rDNA	178	134	1053 (782)	GTR + I + Γ
16S rDNA	165	127	1725 (1039)	GTR + I + Γ
c-mos	52	40	488	K80 + I
cytochrome *b*	412	168	1140	GTR + I + Γ
NADH-1	226	87	957	GTR + I + Γ
RAG-2	106	83	1419	GTR + Γ

for each of the 203 or 198 nodes for the original versus alternative topology, respectively).

Relative molecular dates

Relative molecular dates were obtained by directly fitting molecular sequence data (downloaded from release 131 of GenBank, http://www.ncbi.nlm.nih.gov/Genbank) to the bat supertree topology. These data were often not completely congruent with the topology of the bat supertree. However, if we accept the supertree as the best current complete estimate of bat phylogeny, then these data must have evolved according to that topology and fitting them to the supertree is reasonable. Only genes with a good coverage among bats (i.e., sequences for over 50 species) were collected: the mitochondrial genes for 12S and 16S rDNA, NADH-1, and cytochrome b; and the nuclear genes for oocyte maturation factor Mos (c-mos) and recombination activator protein 2 (RAG-2) (see Table 1).

Manipulation and analysis of the sequence data were performed for each gene independently. Protein-coding genes (cyt b, c-mos, RAG-2 and NADH-1) were aligned by eye. Noncoding sequences (12S and 16S rDNA) were first aligned using Clustal W (Thompson et al. 1994) and improved subsequently by visual inspection. Regions for both non-coding genes that could not be aligned unambiguously were excluded from further analysis. After alignment, the species name for each sequence was synonymized with those on the supertree according to Koopman (1993). Where this could not be achieved unambiguously, the sequence was discarded. The supertree was then pruned to contain only those species for which sequences were available. When a species was represented by multiple sequences, the single terminal species was replaced by an unresolved clade with as many members as specimens for that species. The appropriate model of evolution for each gene was determined using ModelTest version 3.06 (Posada and Crandall 1998) (see Table 1). Although ModelTest will also estimate optimal values for the various parameters of the model indicated (e.g., transition:transversion ratio or shape of the gamma distribution), these values were not used but estimated during the subsequent analysis.

The sequence data were then fitted to the pruned supertree under a maximum likelihood framework using PAUP* version 4.0b10 (Swofford 2002). As mentioned, all relevant parameter values were estimated during the analysis. Note that the data were fitted to the supertree exactly as specified, rather than having the supertree act as a constraint tree that could be searched upon. Thus, polytomies in the supertree (both in the supertree itself and from the addition of multiple-specimen species clades) were essentially taken to represent simultaneous speciation events rather than uncertainty in topology (''hard'' versus ''soft'' polytomies, respectively). A global molecular clock was not assumed for any gene. Instead, dates were estimated assuming local clocks, following the procedures in Bininda-Emonds et al. (1999) and Purvis (1995). Specifically, for each gene, nodal ages were determined in a relative fashion as the ratio of the age of the node to the age of a node ancestral to it. Methodically, these relative nodal ages were obtained by calculating the amount of sequence divergence relative to the next ancestral node that was also specified for that gene. Thus, for any single gene, the molecular age of a given node depends on the ages of nodes ancestral to it, which could be specified by information from any or all of fossil sources, other genes, or even more ancestral nodes dated using the same gene. Essentially, this entire procedure amounts to a continual recalibration of the local molecular clocks.

Fossil dates

Geological site information (geographical location and stratigraphic position) was obtained for 647 bat taxa from 63 sources. We obtained a date in millions of years for a particular site (and therefore taxon) using direct dating methods (such as radiometric or paleomagnetic techniques) either given or cited in the source. Where these were not available, we used references to geological time scales (such as biochronological sequences, epochs, subepochs, or stages). Dates for these were obtained from the 1999 GSA Geologic Time Scale (http://www.geosociety.org/) and McKenna and Bell (1997). Where a range was given for a date, the midrange value was taken. Taxa were then assigned to nodes on the supertree topology. For extinct taxa, we used information from explicit phylogenetic hypotheses given or cited in the source to assign these taxa in the supertree. Where this was not possible, we assigned nodes following the taxonomic arrangements in McKenna and Bell (1997). In general, taxa were held to represent the least inclusive nodal assignment possible. Where there were multiple date estimates of the same node, the earliest date was taken to be representative (recognizing that virtually all fossil estimates will be underestimates of the true divergence time).

Only fossil data providing ''reasonable'' information were used. For example, information that was clearly a significant underestimate as a result of a highly incomplete fossil record was discarded. Thus, dates obtained for 13 nodes in the original topology (26 in the alternative topology) were discarded because an older fossil date existed for a daughter node. Data and references for first fossil occurrences for each node in the Jones et al. (2002) supertree are given in supplementary electronic Appendix 1 available online at http://dx.doi.org/10.1554/04-635.1.s1.

Absolute molecular dates

In the absence of a molecular clock, relative molecular dating cannot provide dates for the basal node of the supertree

TABLE 2. Tests of among-clade diversification rate using four topology-based indices of whole-tree symmetry in bats and other mammals. Values represent the test statistic with the *P* value on the second line for each clade (generated by comparing the value of the statistic to that generated by 1,000,000 Monte Carlo simulations under an ERM model). *n* represents clade size and $\%_{res}$, percentage resolution of the topology. The range of values represents the upper and lower bound generated when the analyses were repeated with 1,000,000 random resolutions of polytomies with different degrees of symmetry. Statistics for carnivores, primates and lagomorphs are given here for comparison and are generated from the supertrees presented in Purvis (1995), Bininda-Emonds et al. (1999), and Stoner et al. (2003).

Clade	*n*	$\%_{res}$	I_c	M^*_π	M^*_Σ	B_1
Bats (original topology)	916	47	8432–8671	−0.75–−0.77	0.61–0.62	456–462
			0.000–0.001	0.000–0.000	0.000–0.000	0.000–0.000
Bats (alternative topology)	916	47	7600–7866	−0.73–−0.74	0.61–0.64	451–457
			0.001–0.003	0.000–0.000	0.000–0.000	0.000–0.000
Carnivora	271	78	1270–1414	−0.59–−0.67	0.64–0.67	130–136
			0.33–0.15	0.01–0.000	0.000–0.01	0.000–0.007
Primates	203	79	1206–1281	−0.49–−0.56	0.68–0.72	128–135
			0.36–0.24	0.27–0.05	0.04–0.38	0.000–0.011
Lagomorpha	80	97	506–510	−0.93–−0.94	0.55–0.56	39–40
			0.001–0.001	0.000–0.000	0.000–0.000	0.008–0.03

and its immediate descendant nodes because the position of the root, and therefore the branch lengths leading from it are arbitrary. We used date estimates for these nodes from eight molecular sources (Kirsch et al. 1995; Springer 1997; Cao et al. 2000; Nikaido et al. 2000, 2001; Bastian et al. 2001; Lin and Penny 2001; Springer et al. 2001) that sampled several different gene sequences from a wide range of mammalian orders and used a molecular clock calibrated by one or more nonbat fossil dates.

Where there was more than one age estimate for a node calculated from the different methods above, we used the median of the single (oldest) fossil date and all the molecular values (i.e., treating the different genes as being independent). Eight nodes in the original topology (alternative: seven nodes) had negative branch lengths (i.e., the parent node was estimated to be younger than its daughter node). In each of these eight cases, all of the nodes in question were given the average of their ages (i.e., using information from all the nodes rather than sinking or elevating the date of one node only). To maintain the topological information in the supertree, 0.1 million years was subtracted from the daughter node in each case. Twenty-six nodes (alternative: 27 nodes) had the same age as their parent node and here we also subtracted 0.1 million years from the daughter node.

Interpolated dates

Together, the above methods provided date estimates for 226 nodes, leaving 204 nodes undated (alternative: 198 nodes). For these, we estimated dates based on the size of the parent node using the formula (following Purvis 1995).

$$\text{date(node)} = \text{date(parentnode)} \times \frac{\log(\text{cladesizeofnode})}{\log(\text{cladesizeofparent})}. \quad (1)$$

Statistics relating to the times of divergence (MYA) for all nodes in the Jones et al. (2002) bat supertree are given in supplementary electronic Appendix 2 available online at http://dx.doi.org/10.1554/04-635.1.s2 and the dated phylogeny in nexus format is given in supplementary electronic Appendix 3 available at http://dx.doi.org/10.1554/04-635.1.s3.

Diversification Patterns

Diversification rates among clades

We used four topology-based indices of whole-tree symmetry (B_1 Shao and Sokal 1990; Colless index I_c Colless 1982; Heard 1992; *M* statistics: M^*_π and M^*_Σ, Moore et al. 2004) to quantify how well the bat topology fitted to expectations generated under an equal-rates Markov (ERM) model of clade growth (Yule 1924; Harding 1971). If nonrandom diversification has occurred then this would be detected by taxonomic imbalance in contemporaneous lineages across the phylogeny. Statistical testing was through Monte Carlo simulation of the null distribution of each statistic using 1,000,000 tree topologies of the same size as the bat supertree, but generated under an ERM model. Polytomies in the analyses may bias the analysis of symmetry depending on how these relationships are resolved (Moore et al. 2004). To incorporate this source of phylogenetic uncertainty in the analyses, polytomies in the supertree were treated as soft (i.e., represent uncertainty about the true branching order at that node) and the analyses were repeated with 1,000,000 random resolutions using the taxon-size sensitive ERM algorithm (Chan and Moore 2005). Phylogenetic uncertainty was also incorporated by running the analyses for both of the two alternative supertree phylogenies. Both these sensitivity analyses provided an upper and lower confidence interval for *P*-values for each of the whole-tree tests of among-lineage diversification rate variation, corresponding to the tail probabilities for the 0.025 and 0.975 frequentiles.

Identifying diversifying clades

To identify particular nodes in the bat topology that showed significant imbalance, we used two topology-based methods. In the first method, the Slowinski-Guyer (1993) test, species diversity contrasts between sister clades (by definition the same age) are compared to those expected under an ERM model. The probability of observing an equal or greater difference in species richness between sister clades is $2r/(r + s - 1)$, where *s* and *r* are the numbers of species in the more or less species-rich clades, respectively (Slowinski and Guyer 1993). This method has been recently criticized for low power

TABLE 3. Bat sister clades with significantly different diversification rates ($P < 0.1$) using different diversification statistics. Node represents nodal number in the original bat supertree topology (Jones et al. 2002) and the first taxa listed in the supertree in each sister clade comparison is given for reference. Δ_1 represents the delta shift-statistic of Moore et al. (2004) and Chan and Moore (2005) and SG the Slowinski-Guyer test. Values represent the *P*-value of the statistic compared to that generated by 1,000,000 Monte Carlo simulations under an ERM model. The upper and lower *P*-values are given where the node involved a polytomy. Relationships significant at the $P < 0.05$ are shown in bold. PTERO represents Pteropodidae; EMBAL, Emballonuridae; RHINO, Rhinolophidae; HIPPO, Hipposideridae; PHYLLO, Phyllostomidae; MOLO, Molossidae; VESP, Vespertilionidae; and IF, interfamilial.

Node	Clade	Sister clade description	Δ_1	SG	Clade sizes
2.03	PTERO	*Paranyctimene* and *Nyctimene*	0.01–0.12	0.00–0.36	1,14
2.30	PTERO	*Plerotes* and *Casinycteris*/*Epomophorus*/*Epomops*	0.09	0.27	1,16
2.51	PTERO	*Harpyionycteris* and *Aproteles*/*Dobsonia*/*Pteropus*	0.06	0.29	2,76
4.08	EMBAL	*Taphozous theobaldi* and rest of *Taphozous*	0.07	0.07	2,9
1.08	IF	Nycteridae and Rhinolophidae/Hipposideridae	0.10	**0.02**	12,120
7.05	RHINO	*Rhinolophus cognatus* and rest of rhinolophids	0.03–0.88	0.00–0.54	2,56
8.09	HIPPO	*Anthops ornatus* and rest of hipposiderids	0.00–0.48	0.00–0.51	1,57
1.14	IF	Noctilionidae and Mormoopidae/Phyllostomidae	0.09	0.42	2,149
11.01	PHYLLO	Desmodontinae and rest of phyllostomids	**0.04**	0.16	3,138
11.17	PHYLLO	*Trachops cirrhosus* and *Tonatia*/*Mimon*/*Phylloderma*	0.03–0.21	0.02–0.09	1,15
11.40	PHYLLO	*Artibeus hartii* and rest of *Artibeus*	**0.04**	**0.04**	1,16
1.17	MOLO	Tomopeatinae and Molossinae	**0.01–0.02**	0.12–0.30	1,80
12.20	MOLO	*Nyctinomops* and rest of molossids	0.09	**0.04**	4,47
1.18	VESP	Miniopterinae and the rest of vespertilionids	0.04–0.88	0.00–0.54	10,306
15.01	VESP	*Harpiocephalus* and rest of Murinae	0.05	0.08	1,14

(Sanderson and Donoghue 1996), poor accuracy (McConway and Sims 2004), and spurious inference of rate shifts in descendant nodes, the ''trickle-down'' effect (Moore et al. 2004).

Instead, likelihood approaches for locating significant diversification rate shifts that incorporate information on the topological distribution of species diversity over the entire tree have been shown to be more accurate and powerful (Moore et al. 2004). We therefore used a second method based on a whole-tree, likelihood-based test, the delta shift-statistic (Δ_1, Moore et al. 2004; Chan and Moore 2005), to locate significant diversification rate shifts in the bat supertree. The delta shift-statistic assesses the probability of a diversification rate shift along the internal branch of a local three-taxon tree comprising of a local outgroup and the two basal-most ingroup clades. Δ_1 is calculated as a function of two likelihood ratios comparing the likelihood of realizing an observed diversity contrast under a homogeneous model (with only one diversification rate parameter) versus a heterogeneous model (with two rate parameters) model. One likelihood ratio is calculated for the root node (involving a comparison between the outgroup and the ingroup), the other for the nested node (involving the comparison between the two ingroup clades). The probability of a diversification rate shift is then derived as a function of these two likelihood ratios, and the three-taxon evaluations are iterated over all internal branches to effectively survey the whole tree for diversification rate shifts (Moore et al. 2004).

Statistical testing of the Slowinski-Guyer test and Δ_1 was achieved by means of Monte Carlo simulation of their null distributions, using 1,000,000 tree topologies of the same size as the bat supertree, but generated under an ERM model. Where either the ingroup or outgroup nodes in the three-taxon set contained a polytomy, the analyses were repeated for each possible resolution, giving an upper and lower bound on the probability value obtained (Chan and Moore 2005). We also repeated the analysis with the alternative supertree phylogeny to assess the dependence of the identified nodes

TABLE 4. Summary statistics for nodal age estimates in different bat families. Node represents nodal number given in the bat supertree topology (see Jones et al. 2002); N_{TAXA}, number of taxa in each clade; N_{DNODE}, number of dated nodes; $\%_{DATED}$, percentage of the number of dated to undated nodes; N_{DATES}, number of date estimates for each clade (including the oldest fossil estimate only); N_{DATES}/N_{TAXA}, proportion of the number of date estimates to clade size; N_{SINGLE}, number of nodes based on only one date estimate; N_{FOS}, number of nodes based solely on fossil date estimates; and N_{MOL}, number of nodes based solely on molecular date estimates.

Node	Clade	N_{TAXA}	N_{DNODE}	$\%_{DATED}$	N_{DATES}	N_{DATES}/N_{TAXA}	N_{SINGLE}	N_{FOS}	N_{MOL}
2.01	Pteropodidae (Old World fruit bats)	166	35	46.1	94	0.57	7	2	30
4.01	Emballonuridae (Sheath-tailed bats)	47	9	28.1	12	0.27	7	5	3
5.01	Megadermatidae (False vampire bats)	5	2	100	2	0.40	2	2	0
6.01	Nycteridae (Slit-faced bats)	12	2	28.7	2	0.17	2	1	1
7.01	Rhinolophidae (Horseshoe bats)	64	4	33.3	8	0.13	3	1	2
8.01	Hipposideridae (Old World leaf-nosed bats)	66	8	33.3	10	0.15	6	5	2
9.01	Natalidae (Funnel-eared bats)	5	2	66.7	4	0.80	1	1	0
10.01	Mormoopidae (Naked-backed bats)	8	6	100	30	3.75	0	0	3
11.01	Phyllostomidae (New World leaf-nosed bats)	141	72	80.0	137	0.97	35	6	50
12.01	Molossidae (Free-tailed bats)	80	19	42.2	30	0.38	10	9	5
1.19	Vespertilionidae (Vesper bats)	268	43	44.8	100	0.37	14	12	16

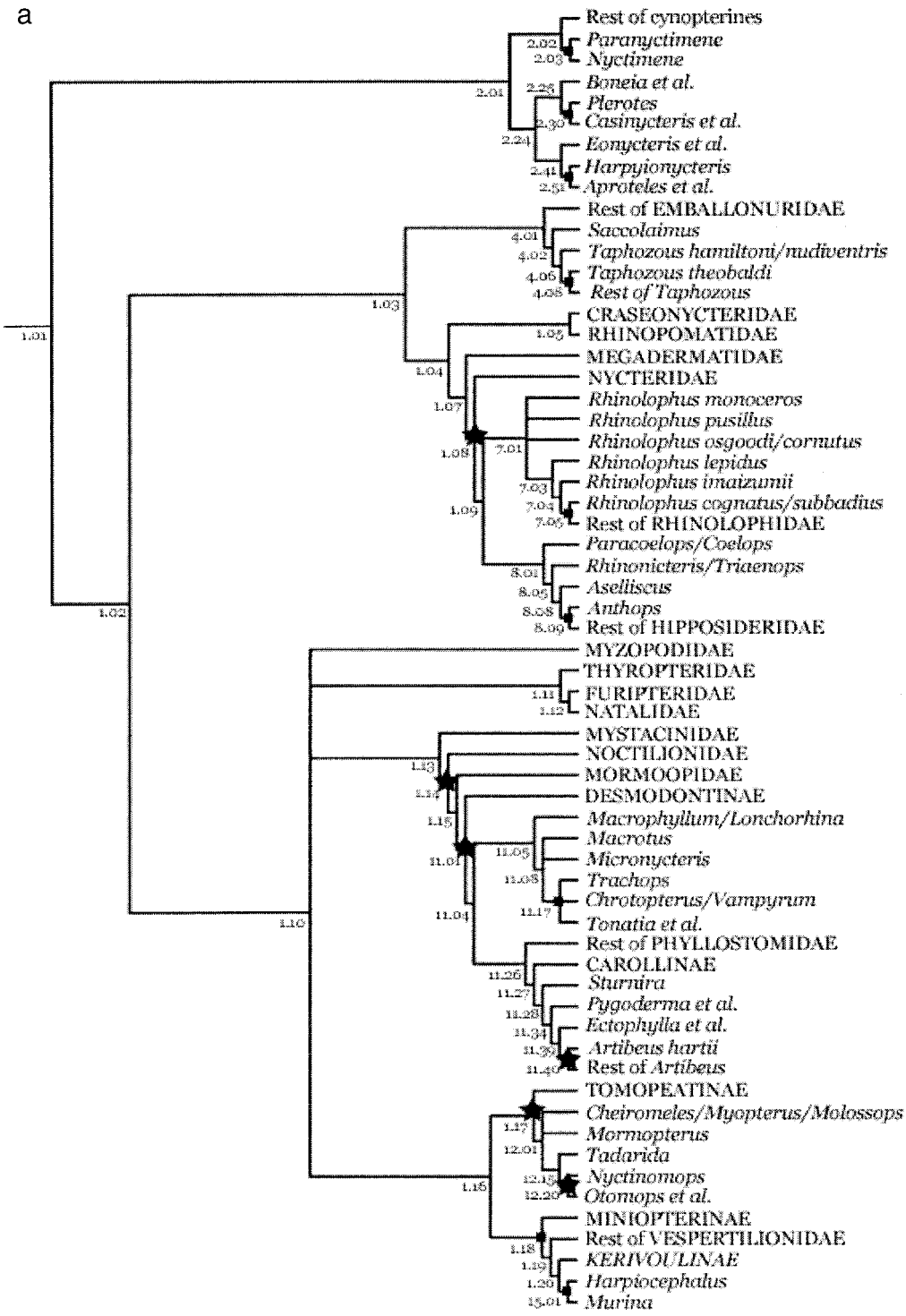

FIG. 1. Diversification rate differences in the (a) original bat supertree (Jones et al. 2002) and (b) the alternative topology. Stars represent nodes with a significantly different diversification rate at $P < 0.05$ level using the delta shift-statistic or the Slowinski-Guyer (1993) test. Solid squares represent differences at $P < 0.1$ level (see Table 3 for statistics). The number below each node represents the original nodal number presented Jones et al. (2002).

on different estimates of the higher-level relationships. Analyses of tree symmetry and identification of diversifying clades were implemented using SymmeTREE version 1.1 (Moore et al. 2004; Chan and Moore 2005).

Other methods of investigating among-clade shifts in diversification use the timing of speciation events to extend the ERM model to explicitly consider both speciation (λ) and extinction (μ) rates, typically against a Constant Rates Markov (CRM) null model (Nee 2001). Here both λ and μ are constant among lineages and through time, where speciation

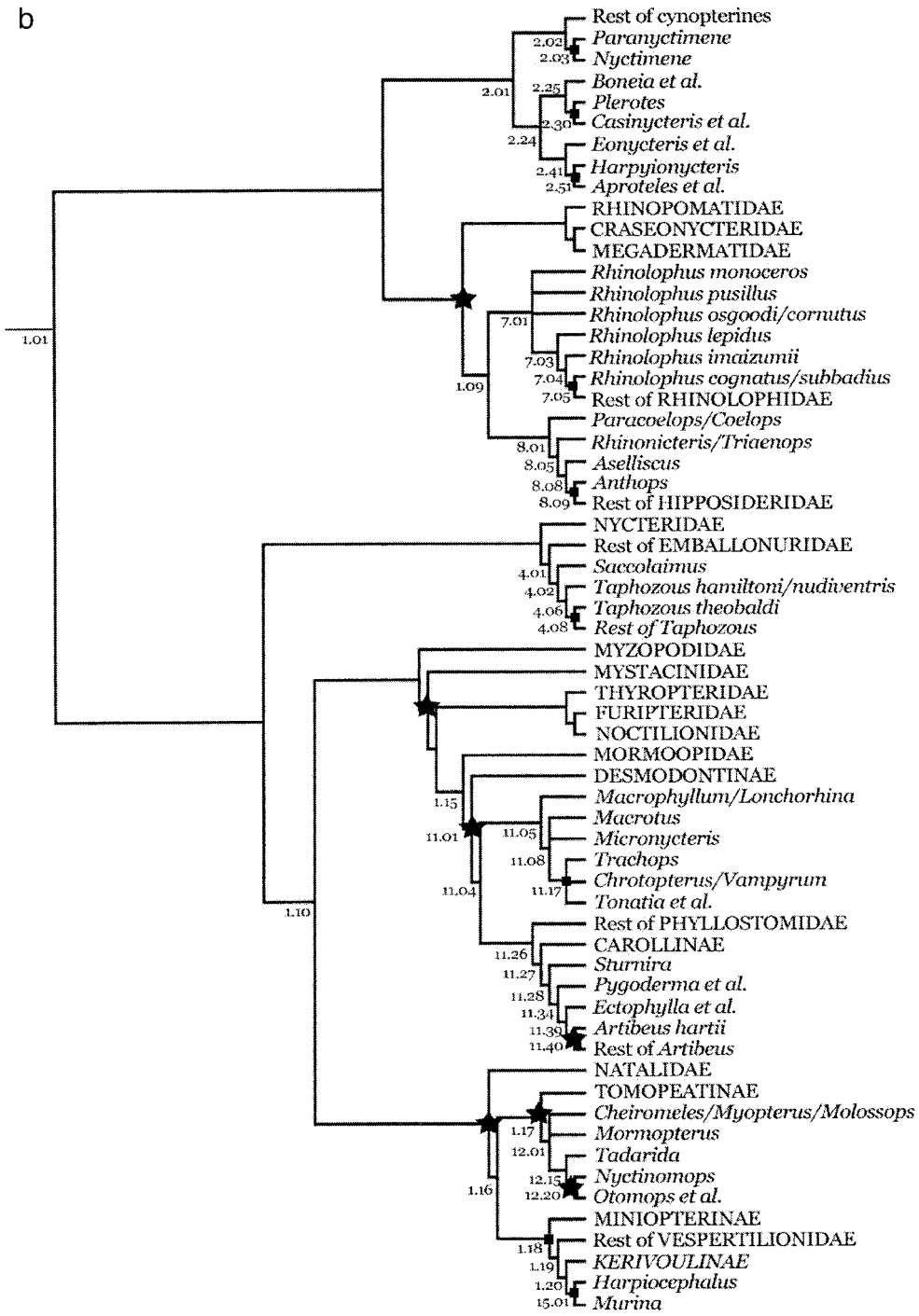

FIG. 1. Continued.

rate is greater than the extinction rate. Estimates of both λ and μ can be made and departures from the null model can be tested either using maximum likelihood (e.g., Nee 2001) or survival analysis approaches (e.g., Paradis 1997). However, we believe that both the low resolution of the supertree and the pure birth process (the null model for the statistical tests) that was used to estimate the ages of nearly half of the nodes, which were unevenly distributed among clades, would unduly influence the among-clade tests. We therefore concentrated on using our temporal estimates of speciation events in a more general way to investigate the timing of diversification across the entire tree (see below).

RESULTS

Diversification Rates among Clades

The whole-tree tests all indicate significant variation in diversification rates among lineages of the bat supertree. Up-

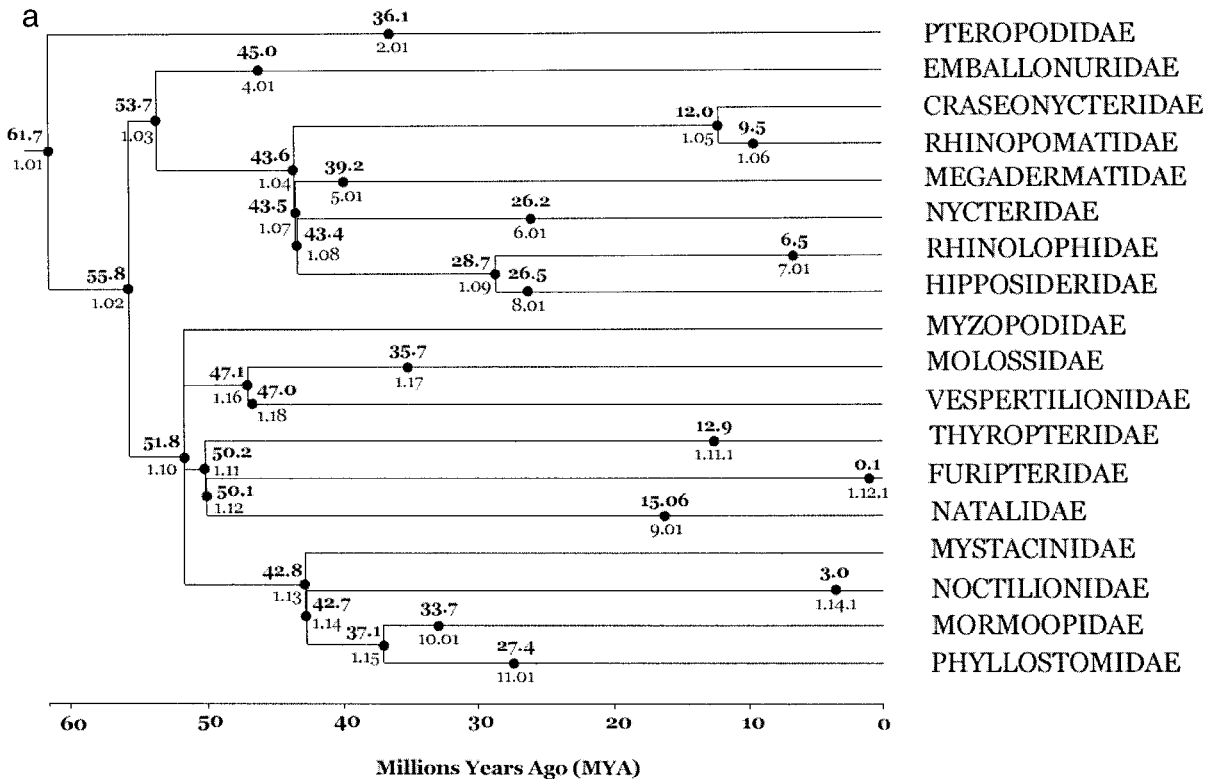

FIG. 2. Dated bat higher-level supertree phylogeny of (a) original bat supertree (Jones et al. 2002) and (b) the alternative topology. Branches are proportional to time (millions of years). The number below each node represents the original nodal number presented Jones et al. (2002), and the number above represents the divergence time (million years ago).

TABLE 5. Family divergence dates. Numbers represent the best estimate of divergence date (million years ago) for the original supertree of Jones et al. (2002; ST_original) or the alternative family level topology of Teeling et al. (2005; ST_alternative). The best estimate is the median of the date estimate or the birth model corrected for negative or equal branch lengths. Type represents the type of date estimate where AM represents absolute molecular date, F fossil and M molecular. The divergence dates represent the time when each family split off from its sister taxa with the divergence date of the crown group given in parentheses.

Node description	ST_original	ST_alternative	Type
Basal node	61.7	57.9	AM
Pteropodidae	61.7 (36.1)	55.8 (24.6)	M
Emballonuridae	53.7 (45.0)	52.1 (46.1)	M
Craseonycteridae	12.0 (12.0)	38.9 (38.9)	—
Rhinopomatidae	12.0 (9.5)	39.0 (19.4)	—
Megadermatidae	43.5 (39.2)	38.9 (38.9)	M,F
Nycteridae	43.4 (26.2)	52.1 (26.1)	M
Rhinolophidae	28.7 (6.5)	34.9 (8.7)	M,F
Hipposideridae	28.7 (26.5)	34.9 (34.8)	M,F
Myzopodidae	51.8 (51.8)	51.6 (51.6)	M,F
Thyropteridae	50.2 (12.9)	42.1 (15.0)	M
Furipteridae	50.1 (0.1)	36.2 (0.1)	M
Natalidae	50.1 (15.1)	51.4 (17.3)	M
Mystacinidae	42.8 (42.8)	46.1 (46.1)	M
Noctilionidae	42.7 (3.0)	36.2 (2.6)	M
Mormoopidae	37.1 (33.7)	38.8 (34.2)	M
Phyllostomidae	37.1 (27.4)	38.8 (28.1)	M
Molossidae	47.1 (35.7)	49.3 (38.2)	M
Vespertilionidae	47.1 (47.0)	49.3 (49.2)	M

per and lower confidence intervals on probability values (incorporating different polytomy resolutions and topologies) were all $P < 0.001$ (after Bonferroni correction for multiple tests) (Table 2).

Identifying Diversifying Clades

Table 3 lists the nodes in the original supertree topology (Jones et al. 2002) where significant shifts in diversification rate have occurred (at the $P < 0.1$ level) under the delta shift-statistic and the Slowinski-Guyer test (although we only consider shifts at the $P < 0.05$ level as significant, those at $P < 0.1$ are informative). The delta shift-statistic suggests that unequivocal diversification rate shifts occurred within both the Phyllostomidae (New World leaf-nosed bats) and Molossidae (free-tailed bats) (Table 3, Fig. 1a). In Phyllostomidae, there are two rate shifts; the first between the Desmodontinae (vampire bats) and the rest of the phyllostomid bats (node 11.01 in Jones et al. 2002) and the second between *Artibeus hartii* and rest of *Artibeus* (subfamily Stenodermatinae) (node 11.40). The significant shift in Molossidae was found between the two subfamilies Tomopeatinae and Molossinae (node 1.17) (Table 3, Fig. 1a). Other shifts were also identified within Pteropodidae (Old World fruit bats), Rhinolophidae (horseshoe bats), Hipposideridae (Old World leaf-nosed bats), and Vespertilionidae (evening bats), but their significance was sensitive to incomplete phylogenetic resolution. Several other shifts were also marginally significant, for example, those between *Harpyionycteris* and the clade

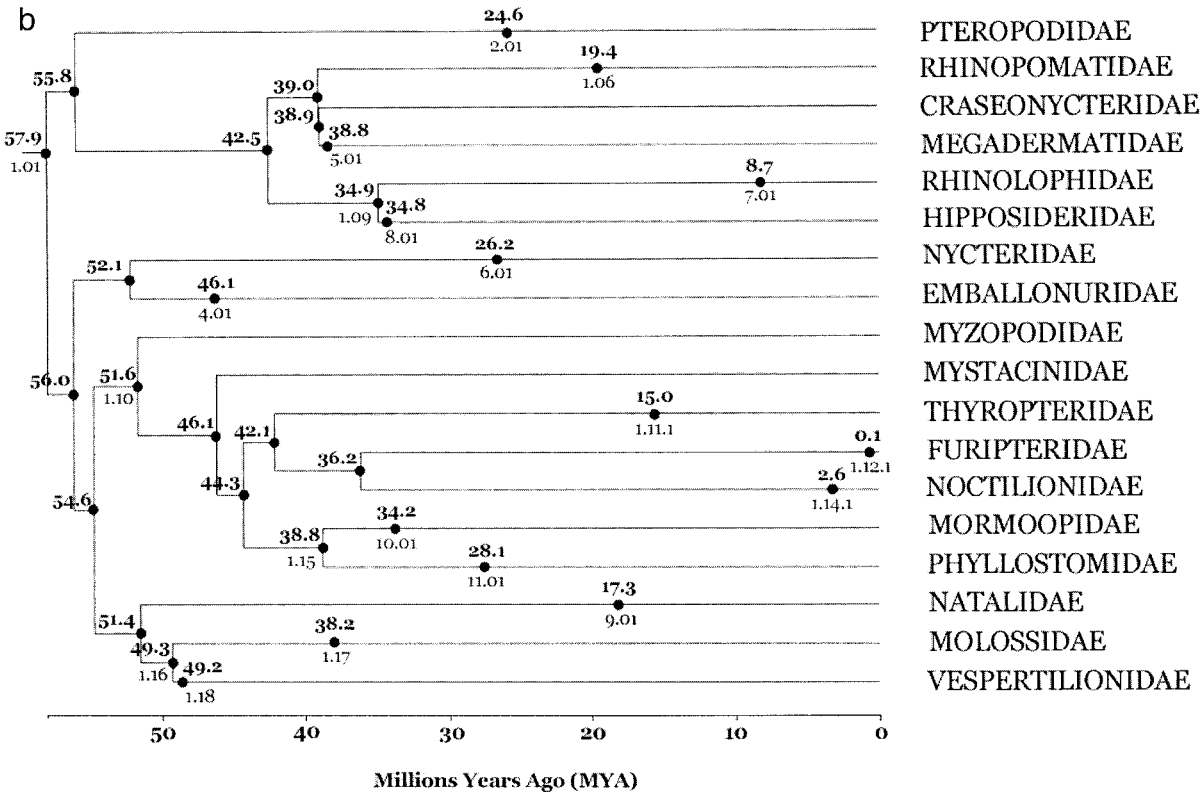

FIG. 2. Continued.

containing the genera *Aproteles*, *Dobsonia* and *Pteropus* (Pteropodidae) (node 2.51, $P = 0.06$); between *Taphozous theobaldi* and the rest of *Taphozous* (Emballonuridae, sheath-tailed bats) (node 4.08, $P = 0.07$), within Murininae (Vespertilionidae) between *Harpiocephalus harpia* and the genus *Murina* (node 15.01, $P = 0.05$), and within Molossidae between *Nyctinomops* and rest of the molossids (node 12.20, $P = 0.09$) (Fig. 1a). There was no evidence for a significant shift between the suborders Megachiroptera and Microchiroptera (node 1.01) ($P = 0.30$).

Results from the delta shift-statistic are largely congruent with the Slowinski-Guyer (1993) test, although some shifts under the latter test lost significance (node 11.01 and node 1.17). Interestingly, the Slowinski-Guyer test identified nodes between families as the significant shifts (Table 3), perhaps demonstrating the trickle-down effect of this test biasing the probability estimates of ancestral nodes. Additionally, the shift between *Nyctinomops* and rest of molossids was recognized as significant using the Slowinski-Guyer test although only found to be marginally significant with the shift-statistic ($P = 0.09$). Results using the alternative phylogeny were identical (Fig. 1b), except the two interfamilial shifts were no longer applicable because the sister-taxa relationships were not present in this topology. However, three of the alternative interfamilial nodes demonstrated significant diversification shifts. These were as follows: (1) between Mystacinidae (short-tailed bats) and the node containing Phyllostomidae, Mormoopidae (nacked-backed bats), Noctilionidae (bulldog bats), Furipteridae (smoky bats), and Thyropteridae (disk-winged bats) ($P_{\Delta 1} = 0.03$, $P_{SG} = 0.44$, $n = 1, 155$), (2) between Natalidae (funnel-eared bats) and the node containing Molossidae and Vespertilionidae ($P_{\Delta 1} = 0.02$, $P_{SG} = 0.19$, $n = 5, 397$), and (3) between the node containing Megadermatidae (false vampire bats), Craseonycteridae (bumblebee bat), and Rhinopomatidae (mouse-tailed bats) versus that containing Rhinolophidae and Hipposideridae ($P_{\Delta 1} = 0.08$, $P_{SG} = 0.01$, $n = 9, 130$) (Fig. 1b).

Identifying Diversification Times

Fossil or molecular evidence directly dated 53% of the nodes in the phylogeny, which were unevenly distributed among clades (Table 4). The proportion of dated to estimated nodes was highest in Phyllostomidae, Pteropodidae, Mormoopidae, Megadermatidae, and Natalidae (although the latter three clades have only a small number of nodes to date) and lowest in the Emballonuridae, Nycteridae, Rhinolophidae, and Hipposideridae (Table 4). Out of the 226 directly calculated dates, 128 were based only on the relative amount of molecular sequence divergence calibrated to dated ancestral nodes, 50 nodal dates were based on both molecular and direct fossil evidence, and 47 were based only on direct fossil evidence; 58.8% of the dates overall were based on data from more than one estimate. The contribution of fossil information to the nodal date estimate varied between clades. For example, within Molossidae, Phyllostomidae, Pteropodidae, Vespertilionidae, and Rhinolophidae reliance on fossil information alone was low.

The divergence times of the majority of the higher-level nodes could be directly calculated using either fossil or mo-

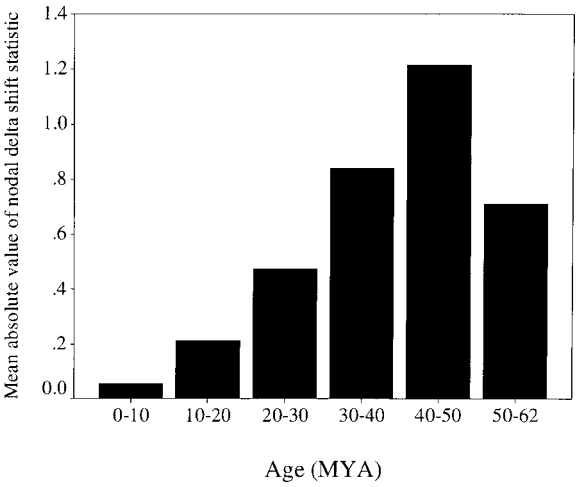

FIG. 3. Mean absolute value of nodal delta shift statistic within each 10 million year time bin across the original bat supertree (Jones et al. 2002). Results with the alternative topology were not qualitatively different.

lecular evidence (Fig. 2a,b). Only the timing of the splits of the families Craseonycteridae and Rhinopomatidae (nodes 1.05 and 1.06) had to be estimated from a pure birth model (supplementary electronic Appendix 2). Because of a lack of suitable fossils, we calculated the age for the basal node of the supertree at 61.7 million years ago (MYA) using absolute molecular dates for the divergence time of the crown group (i.e., the most recent common ancestor of all extant species and all its descendants). This is a minimum estimate for the divergence time for the order (the timing of the split from its sister clade will be earlier). The divergence dates indicate that many families were established early in the evolutionary history of the group (median family age 43.4 MYA) (Table 5). Here we define family age as the time of the divergence of each family from its sister taxa (e.g., node 1.09 at 28.7 MYA dates both the divergence of Rhinolophidae and Hipposideridae, Fig. 2a). Using the alternative supertree topology, the divergence dates are very similar, with the exception of Rhinopomatidae and Craseonycteridae (Table 5). As these family divergence times were estimated from the birth model, they are more dependent on their placement in the phylogeny. Using the alternative topology, these families occupy a more basal position and so their divergence dates are estimated as being earlier.

Using both the calculated and the estimated nodal dates, we examined the mean of the absolute value of the delta shift statistic for nodes in the topology in 10 million year time intervals (Fig 3). We obtained the largest values from 40–50 MYA and 30–40 MYA. Mean values in the shifts in diversification rates are significantly different between time intervals (one-way ANOVA $F_{5,423} = 22.90$, $P < 0.001$) and the mean values in the 40–50 MYA interval are significantly larger than in the first three time intervals (spanning 0–30 MYA, Tukey test $P < 0.01$) and the mean values of the 30–40 MYA interval are significantly different from the first two time intervals (0–20 MYA, Tukey test $P < 0.001$). Results using the alternative topology were not quantitatively different.

We examined the distribution of species in extant lineages in clades that were present 30 MYA to understand which lineages were responsible for the large diversification rate shifts within these time intervals (Fig. 4). The lineage ultimately leading to Vespertilionidae (excluding Miniopterinae) contains the most extant species (306) with the lineages leading to Phyllostomidae, Rhinolophidae plus Hipposideridae, Pteropodidae (excluding the cynopterines and nyctimenes), Molossidae, and Emballonurinae containing the majority of the rest of the order. Lineages such as those leading to Myzacinidae, Myzopodidae, and Megadermatidae show particularly low species richness.

DISCUSSION

Among-clade diversification rates vary significantly in bats, a pattern common in many other Metazoa (e.g., Chan and Moore 2002; Purvis and Agapow 2002). However, bats have had a greater degree of variation in their among-clade diversification rate than other mammalian clades hitherto studied. For example, the primate supertree does not show significant imbalance (Purvis et al. 1995; Moore et al. 2004) and the whole-tree symmetry statistics for primates, carnivores, and lagomorphs (Table 2) are generally lower than those for bats (see also Chan and Moore 2002). The bat supertree topology is the least resolved supertree in Table 2 and this may bias the reported imbalance scores. However, this seems unlikely, because the methods employed here directly incorporate the phylogenetic uncertainty due to unresolved nodes in the probability estimates. Additionally this result is independent of the different arrangement of higher level relationships proposed by Teeling et al. (2005). The significance of the whole-tree tests of diversification rate variation can also be used to suggest where in the tree diversification occurred because these statistics have different sensitivities to diversification occurring at different places in the topology (Chan and Moore 2002; Moore et al. 2004). Going from left to right, the statistics in Table 2 are increasingly sensitive to changes in diversification rate closer to the tips of the topology (Moore et al. 2004; Chan and Moore 2005). This suggests that bat diversification rate change has occurred closer to the tips of the tree rather than at the more basal nodes (i.e., the I_c statistic *P*-value is higher than the other three statistics, although all are highly significant).

Our results indicate that bats have undergone a number of significant diversification rate shifts, especially so within Phyllostomidae and Molossidae, although several other clades have marginally significant shifts in diversification rate. We place more emphasis here on the results derived from the likelihood-based shift statistics because of the problems associated with the power, accuracy and independence of the Slowinski-Guyer test (McConway and Sims 2004; Moore et al. 2004). Despite the lack of previous formal statistical analyses, earlier studies have proposed a number of mechanisms that may have driven radiations within at least some of the clades. For example, the extremely diverse morphologies of the phyllostomids have long been hypothesized to be the results of an adaptation to different feeding ecologies (specifically, adaptations to eat fruit, pollen, nectar, or other vertebrates and escaping the restraints of insectivory)

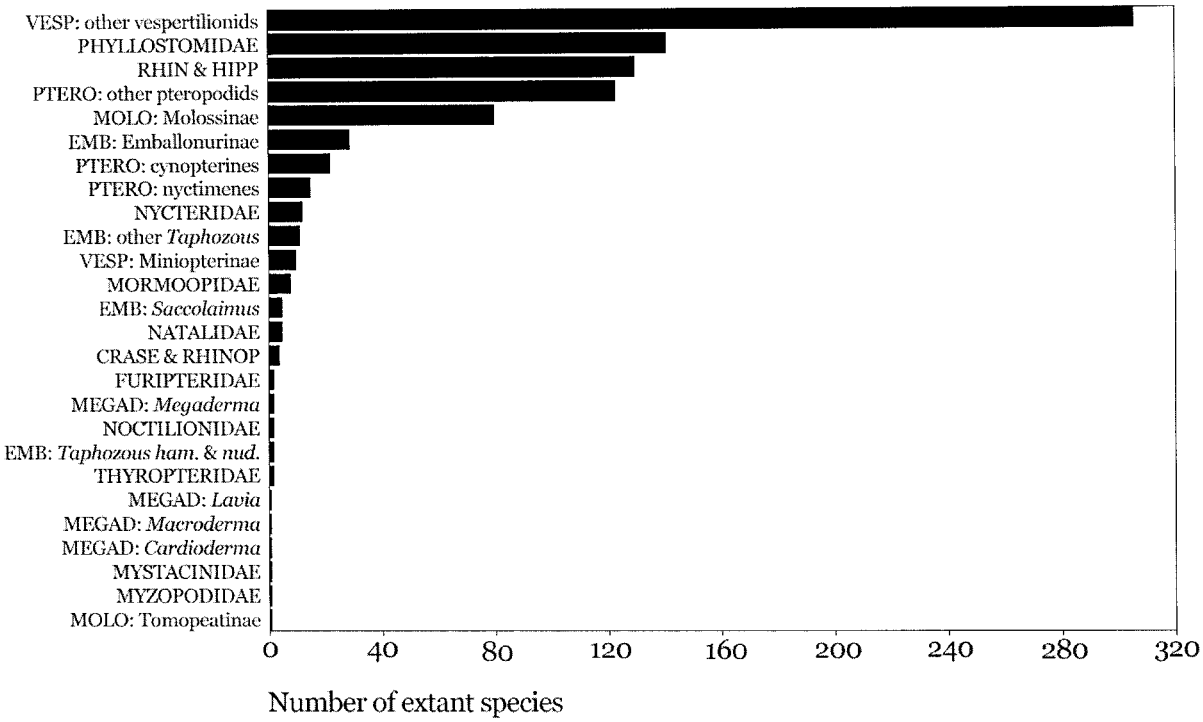

FIG. 4. Hollow curve distribution of the number of extant species in bat lineages present 30 million years ago, based on the original topology of Jones et al. (2002). *Taphozous ham.* represents *Taphozous hamiltoni* and *T. nud.*, *Taphozous nudiventris*. Family names are given in upper case for which EMB represents Emballonuridae; CRASE, Crasonycteridae; RHINOP, Rhinopomatidae; MEGA, Megadermatidae; RHIN, Rhinolophidae; HIPP, Hipposideridae; MOLO, Molossidae; and VESP, Vespertilionidae.

(Ferrarezzi and Gimenez 1996; Freeman 2000; Wetterer et al. 2000; Simmons and Conway 2003). Although we demonstrate statistically that phyllostomids have indeed undergone significant shifts in diversification rates, our tests do not allow us to determine a possible mechanism. More explicit hypotheses testing within Phyllostomidae are deserved, although beyond the scope of the present study.

We do not find evidence that diversification rates in the two suborders are statistically different, although an adaptive radiation in Microchiroptera has been hypothesized by Simmons and Geisler (1998), who suggest that this radiation was driven by the coupling of ventilation and flight to provide a low cost echolocation system that enabled microchiropteran bats to use continuous aerial hawking as a foraging strategy. An adaptive radiation has also been hypothesized for both the rhinolophids and hipposiderids, through the evolution of a high duty-cycle echolocation system from a low duty-cycle ancestor (Simmons and Conway 2003). This type of echolocation allows the detection of fluttering insects in dense forest, close to vegetation or the ground, which is proposed to have opened up novel foraging niches (Schnitzler and Kalko 1998). However, the power of the current analysis to test for a significant rate shift in rhinolophids and hipposiderids was reduced because of the poor resolution in this part of the supertree. It is likely that as phylogenetic information in this area of the tree improves, then the power of these analyses to detect significant shifts will increase.

Investigating correlates of diversification rate shifts within bats is challenging because it seems unlikely that variation in a single trait is responsible for all diversification rate shifts that we observe. It may be that different key innovations are responsible for different events. This seems to be especially true in bats. Evidence so far is consistent with this hypothesis; our previous work has failed to find simple associations of bat diversification with any particular morphological or life-history variable (Isaac et al. 2005). For example, neither body size, wing morphology, nor reproductive rate significantly predicts species richness within bats. Clearly, further detailed analyses are required. One avenue for further investigation is to examine the extent to which coevolution with other clades is responsible for shifts in bat diversification rates. For example, using a dated supertree of all extant angiosperm families, Davies et al. (2004b) found the number of diversification rate shifts of flowering plants to be highest between 25 and 40 MYA overlapping with that of the bats. Although this hypothesis needs to be rigorously examined, these patterns may suggest that the increase in the diversification of flowering and fruiting plants caused a correlated increase in the diversification of fruit and flower-eating bats (a major group of which are Phyllostomidae) and perhaps insect-eating bats (through an increase in insect pollinators). More powerful tests of the temporal divergences will need a larger taxonomic coverage of molecular sequence data to directly calculate the missing divergence dates in the phylogeny. However, although the divergence dates presented are only based on only half the nodes in the phylogeny, they do agree with other higher-level independent estimates. For example, the higher-level divergence times are very consistent with Teeling et al.'s (2005) estimates from 13 nuclear genes using

Bayesian dating methods (Thorne et al. 1998; Kishino et al. 2001).

Our analyses have gone significantly beyond Van Valen's (1979) original hypothesis and we anticipate further exciting developments with more complete and accurate phylogenetic information and more detailed examinations of diversification rate correlates. For example, it is suggested that flight is the key innovation that has allowed bats to diversify in relation to other mammalian clades (e.g., Helgen 2003). This clearly should be tested, although demonstrating that bats have showed a significantly higher diversification rate from their sister clade needs to be done first. Investigating diversification rates among different orders will have to wait on a better understanding of the pattern and timing of mammalian evolution than is currently available.

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