Pp. 27-42, In Bat Biology and Conservation (T.H. Kunz and P.A. Racey, eds.). 1998. Smithsonian Institution Press, Washington.

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In the Minotaur's Labyrinth

Phylogeny of the Bat Family Hipposideridae

WIESLAW BOGDANOWICZ AND ROBERT D. OWEN

The family Hipposideridae is composed of nine Recent genera with about 65 species, which are widespread throughout warm areas of the Old World from western Africa east to the New Hebrides and extend only marginally into the Palaearctic (Corbet and Hill 1991, 1992; Koopman 1994). The genus *Hipposideros* has about 50 species; the other genera either are monotypic *(Anthops, Cloeotis, Paracoelops, Rhinonycteris)* or have 2 species *(Asellia, Aselliscus, Coelops, Triaenops)*. Hipposiderid fossils are known from the middle Eocene of Europe (Sigé and Legendre 1983; Sigé 1991), the early Oligocene of Arabo-Africa (Sigé et al. 1994), the late Oligocene of Australia (Archer et al. 1994), and probably the Miocene of Asia (K. F. Koopman, in litt.).

During the past 150 years hipposiderids have attracted the attention of numerous taxonomists (summarized by Hill 1963). The most prominent studies in this century were those by Tate (1941) and Hill (1963) of the genus *Hipposideros* and by Hill (1982) of the genera *Rhinonycteris, Cloeotis,* and *Triaenops.* Their work resulted in recognition of 11 (Tate 1941) or 6 (Hill 1963) supraspecific groups within the genus *Hipposideros.* Most of the more recent researchers (e.g., Jenkins and Hill 1981; Kock and Bhat 1994; Koopman 1994) either have accepted Hill's point of view or have made only minor changes to his 1963 classification. However, the question arises as to what extent Hill's carefully arranged, but nevertheless intuitive, species groups reflect phylogenetic history.

More importantly, none of the previous studies evaluated phylogenetic affinities within the entire family. The aim of our chapter is to fill this gap, although the lack of well-preserved materials for some taxa makes our analysis incomplete. Nevertheless, it is a first step toward a comprehensive revision of phylogenetic relationships among hipposiderids. We also evaluated different hypotheses concerning the geographic center of origin for the family and the monophyly of the genus *Hipposideros.* These assessments were made through phylogenetic analyses of metrical and discrete-state characters of the cranium, dentition, and external morphology.

Materials and Methods

Species, Specimens, and Measurements

Our study was based on 57 species and 702 adult specimens (skins and skulls), each of which had no or few missing char-

Table 2.1
Common-Part-Removed Analysis

Species	*n* (sexed + unsexed)	R^2	Species	*n* (sexed + unsexed)	R^2
Anthops ornatus	3 + 1	0.936	*Hipposideros inexpectatus*	1 + 0	0.952
Asellia patrizii	3 + 0	0.977	*Hipposideros jonesi*	17 + 0	0.986
Asellia tridens	10 + 0	0.970	*Hipposideros lankadiva*	8 + 0	0.964
Asselliscus stoliczkanus	9 + 0	0.984	*Hipposideros larvatus*	29 + 0	0.985
Aselliscus tricuspidatus	10 + 0	0.983	*Hipposideros lekaguli*	3 + 0	0.991
Cloeotis percivali	11 + 0	0.970	*Hipposideros lylei*	12 + 0	0.985
Coelops frithi	18 + 0	0.854	*Hipposideros macrobullatus*	4 + 0	0.988
Coelops robinsoni	2 + 0	0.796	*Hipposideros maggietaylorae*	13 + 0	0.976
Hipposideros abae	15 + 0	0.986	*Hipposideros marisae*	9 + 0	0.989
Hipposideros armiger	26 + 0	0.978	*Hipposideros magalotis*	11 + 0	0.978
Hipposideros ater	11 + 0	0.987	*Hipposideros muscinus*	11 + 0	0.983
Hipposideros beatus	16 + 0	0.992	*Hipposideros obscurus*	12 + 0	0.987
Hipposideros bicolor	8 + 0	0.984	*Hipposideros papua*	8 + 0	0.985
Hipposideros caffer	59 + 0	0.989	*Hipposideros pomona*	11 + 0	0.977
Hipposideros calcaratus	11 + 0	0.985	*Hipposideros pratti*	14 + 0	0.976
Hipposideros camerunensis	3 + 0	0.979	*Hipposideros pygmaeus*	10 + 0	0.992
Hipposideros cervinus	30 + 0	0.993	*Hipposideros ridleyi*	5 + 0	0.992
Hipposideros cineraceus	10 + 0	0.988	*Hipposideros ruber*	45 + 0	0.986
Hipposideros commersoni	11 + 0	0.969	*Hipposideros sabanus*	3 + 0	0.978
Hipposideros corynophyllus	1 + 0	0.969	*Hipposideros semoni*	7 + 0	0.979
Hipposideros curtus	8 + 0	0.987	*Hipposideros speoris*	11 + 0	0.984
Hipposideros cyclops	12 + 0	0.978	*Hipposideros stenotis*	4 + 0	0.984
Hipposideros diadema	27 + 0	0.977	*Hipposideros terasensis*	25 + 0	0.979
Hipposideros dinops	12 + 0	0.969	*Hipposideros turpis*	11 + 0	0.983
Hipposideros dyacorum	10 + 0	0.983	*Hipposideros wollastoni*	3 + 0	0.991
Hipposideros fuliginosus	10 + 0	0.992	*Rhinonycteris aurantius*	10 + 0	0.987
Hipposideros fulvus	10 + 0	0.986	*Triaenops furculus*	5 + 4	0.989
Hipposideros galeritus	12 + 0	0.994	*Triaenops persicus*	25 + 0	0.977
Hipposideros halophyllus	2 + 0	0.982			

Notes: This table lists ingroup taxa (Hipposideridae), number of specimens (*n*), and coefficient-of-determination (R^2) values adjusted for degrees of freedom from linear regression of each ingroup taxon on a multiple-member outgroup (*Rhinolophus celebensis*, $n = 12$; *R. clivosus*, $n = 10$; *R. hipposideros*, $n = 12$; *R. malayanus*, $n = 8$; and *R. sinicus*, $n = 9$). When multiplied by 100, R^2 indicates percentage of original variance explained by the outgroup.

acters (Table 2.1). Adults were recognized by fused epiphyses in wing bones. *Hipposideros schistaceus* was found to be morphologically very similar to or even indistinguishable from *H. lankadiva* (P. J. J. Bates, personal communication; our observations); consequently, it was not treated as a distinct species. Space limitation precludes a list of specimens examined, but this list is available on request from the first author via Internet at wieslawb@robal.miiz.waw.pl.

A total of 45 cranial, dental, and external characters were measured with a Sylvac electronic caliper directly connected to a PC-compatible laptop computer for automatic data capture. The width and height of the foramen magnum (not included in Table 2.2) were used to calculate the foramen magnum area according to the formula given by Radinsky (1967). Measurements were taken to the nearest 0.01 mm for cranial and dental characters and to the nearest 0.1 mm for external characters. The length of the hindfoot included the claws. Other measurements followed Freeman (1981), Rautenbach (1986), and Bogdanowicz (1992). Forearm lengths given in *Results* are from Koopman (1994).

Transformations

All continuous values were transformed to their natural logarithms, and the value of each character was calculated as the average of the means for males and females. Where possible, samples from single or neighboring populations were used for each species. For two endemic species without evident sexual dimorphism (*Anthops ornatus* and *Triaenops furculus*), unsexed specimens also were used.

The common-part-removed transformation (Wood 1983) was applied to remove the portion of variance accounted for by regression onto selected rhinolophid taxa. Because Rhinolophidae is the sister-taxon to the Hipposideridae

Table 2.2
Size-Out Analysis

Character	PC1	PC2	PC3	PC4
Greatest skull length	0.997	–0.023	0.006	–0.026
Condylocanine length	0.997	–0.015	0.022	–0.020
Least interorbital breadth	0.822	0.300	0.256	–0.004
Zygomatic breadth	0.984	0.059	–0.074	–0.053
Mastoid breadth	0.976	0.116	0.115	–0.029
Breadth of braincase	0.976	0.094	0.117	–0.020
Breadth of nasal swellings	0.964	–0.076	–0.126	0.162
Height of braincase (excluding bullae)	0.975	–0.027	0.100	–0.091
Length of maxillary toothrow	0.991	–0.029	–0.051	–0.030
Length of upper molariform row	0.990	–0.023	–0.080	–0.020
Width across upper canines	0.976	–0.043	–0.132	0.054
Height of upper canine	0.974	0.078	–0.027	–0.041
Width across upper third molars	0.981	–0.029	–0.106	0.020
Length of upper third molar	0.947	–0.150	–0.115	0.017
Width of upper third molar	0.970	–0.080	–0.102	–0.008
Supraorbital length	0.938	–0.140	–0.026	0.153
Palatal length	0.926	0.136	–0.101	0.008
Area of foramen magnum	0.922	0.115	0.209	–0.187
Bullar length	0.955	0.010	0.164	0.176
Bullar width	0.898	0.200	0.141	0.246
Greatest length of mandible	0.995	–0.016	–0.059	–0.013
Length of mandibular toothrow	0.992	–0.015	–0.053	–0.024
Postdental length	0.991	0.015	–0.060	–0.000
Height of mandibular ramus	0.968	0.019	–0.140	–0.047
Height of lower canine	0.968	0.119	–0.096	–0.006
Coronoid–angular distance	0.977	0.021	–0.143	–0.027
Length of moment arm of temporal	0.989	0.038	–0.066	–0.015
Length of moment arm of masetter	0.951	–0.077	–0.239	–0.037
Forearm length	0.983	0.002	–0.014	–0.015
Third digit, metacarpal length	0.972	–0.027	–0.021	–0.010
Third digit, first phalanx length	0.901	0.340	0.011	–0.041
Third digit, second phalanx length	0.909	–0.248	0.088	–0.178
Fourth digit, metacarpal length	0.987	–0.036	0.038	–0.030
Fourth digit, first phalanx length	0.959	0.065	–0.022	–0.117
Fourth digit, second phalanx length	0.919	–0.241	0.139	–0.091
Fifth digit, metacarpal length	0.972	–0.124	0.143	–0.087
Fifth digit, first phalanx length	0.952	0.143	–0.070	–0.095
Fifth digit, second phalanx length	0.922	–0.192	0.128	–0.156
Head and body length	0.976	0.042	0.027	–0.012
Tail length	0.522	0.753	–0.152	0.126
Ear length	0.828	0.064	0.375	0.231
Tibia length	0.978	0.004	0.078	–0.018
Hindfoot length	0.970	–0.127	0.040	–0.030
Greatest breadth of anterior noseleaf	0.856	–0.366	0.015	0.272
Greatest breadth of horseshoe (including secondary leaflets)	0.901	–0.288	–0.081	0.247
All characters, variance explained	(89.9%)	(3.1%)	(1.5%)	(1.1%)

Note: Data are character loadings for the first four principal components (PC)—and, in parentheses at the end of the table, the percentages of variance they explain—from principal-components analysis of the correlation matrix. Analysis was based on 57 taxa of the Hipposideridae and the average of five species of *Rhinolophus (R. celebensis, R. clivosus, R. hipposideros, R. malayanus,* and *R. sinicus).*

(e.g., Novacek 1991), this regression function provided an estimate of ancestral hipposiderid morphology. In this study, the vector of character values for each hipposiderid species was regressed separately onto the means of those for *Rhinolophus celebensis, R. clivosus, R. hipposideros, R. malayanus,* and *R. sinicus.* For each ingroup taxon, the vector of residuals was retained. These vectors were combined and used in further calculations in the form of a transformed data matrix.

Another method used was a "size-out" procedure. After averaging the $\log_e$-transformed values, a correlation matrix was calculated and a principal component analysis was performed on the matrix. From this, the matrix of projections of each species of each component was calculated. The first principal component, which primarily reflected size relationships, was then deleted from the matrix, and the remaining principal component scores were taken to be character-state values for a newly created suite of characters. The foregoing calculations were made using the multiple linear regression analysis and factor analysis procedures from the SPSS for Windows package (Norušis 1993).

Phylogenetic Analyses

MAXIMUM-LIKELIHOOD METHOD. The common-part-removed and size-out data matrices were subjected to the CONTML procedure of PHYLIP (Felsenstein 1993), which estimates phylogenies by the restricted maximum-likelihood method based on the Brownian motion model. This algorithm, used primarily for genetic distance data, makes four assumptions concerning the data: (1) the lineages evolve independently; (2) after lineages separate, their genetic (and morphometric) evolution proceeds independently; (3) drift, rather than selection, is the cause of evolutionary change; and (4) each character drifts independently. These assumptions, although never met absolutely in our study (or probably in any phylogenetic study), have been discussed more thoroughly by Felsenstein (1981) and by Bogdanowicz and Owen (1992). In each case, we used global optimization in search for the best tree, which resulted in about 15,000 tree topologies being compared each time. For both analyses, *Rhinolophus celebensis, R. clivosus, R. hipposideros, R. malayanus,* and *R. sinicus* were included to provide a root for the tree (Novacek 1991). In the common-part-removed data, *Rhinolophus* spp. were represented by a vector of zeros (Bogdanowicz and Owen 1992). Because results are dependent on the order in which the species are encountered in the data set, each analysis was repeated 50 times with different orderings of the input taxa. To compare trees and define areas of congruence, we used the majority-rule consensus procedure. The majority-rule consensus tree consists of all groups that occur more than 50% of the time (CONSENSE program of PHYLIP; Felsenstein 1993).

PARSIMONY ANALYSIS. The analysis was based on a set of as many as 30 possibly discrete-state cranial, dental, and external characters (Appendix 2.1), scored from each adult specimen. The ingroup included 57 species and eight of the nine extant genera of the Hipposideridae. Multiple outgroup taxa were used to polarize the character states, enhancing the prospect of correctly identifying autapomorphic features in the outgroup. The characters for analysis were selected after their extensive evaluation from a large series of specimens. The outgroup was composed of the sister-family Rhinolophidae, represented by *Rhinolophus celebensis, R. coelophyllus, R. hipposideros, R. luctus, R. malayanus,* and *R. sinicus.* Megadermatidae *(Cardioderma cor, Megaderma lyra,* and *M. spasma)* and Nycteridae *(Nycteris hispida, N. grandis,* and *N. thebaica)* were used as further outgroup taxa. The Rhinopomatidae *(Rhinopoma microphyllum)* completed the outgroup (see Novacek 1991). A hypothetical ancestor of the Hipposideridae was designated, and all character states were polarized by the outgroup comparison method of Maddison et al. (1984).

Cladograms were constructed using the branch-and-bound algorithm (Hendy and Penny 1982), with the option for reconsidering an order of species that is included in PHYLIP version 3.5 under UNIX (Felsenstein 1993). As many as 31,286 most-parsimonious trees were obtained during a single run for 10,000,000 possible trees. To compare trees and define areas of congruence, we again used the majority-rule consensus procedure. In a final consensus tree, however, we also included groups that occur less than 50% of the time, working downward in their frequency of occurrence, so long as they continue to resolve the tree and do not contradict more frequent groups (CONSENSE program of PHYLIP; Felsenstein 1993). In this respect, the method is similar to the Nelson consensus method (Nelson 1979) although not identical (Felsenstein 1993). Tree lengths, consistency, and retention indices were calculated by Hennig86 version 1.5, using the *mhennig** and *bb** options (Farris 1988). These parameters may have been slightly underestimated because of an overflow of the available tree space in the software used.

Morphological Dispersion

Morphological dispersion of the fauna may be determined by calculating each taxon's average phenetic distance from every other taxon in the fauna, summing the averages, and computing the faunal average (Findley 1976; Freeman 1981; Bogdanowicz 1992). In our studies, the average taxonomic distances (NTSYS-pc package; Rohlf 1993) between every

pair of species in a fauna were computed based on a matrix of standardized residuals. The Kruskall–Wallis nonparametric test was used to evaluate differences among average faunal values. Because no nonparametric multiple-range test exists for unequal sample sizes, the Mann–Whitney *U*-test was conducted on all pairwise combinations of four faunas (nonparametric tests procedure of the SPSS package; Narušis 1993). Geographic affiliations of hipposiderid groups were based on Wallace's zoogeographic divisions (Lincoln et al. 1982).

Results

Common-Part-Removed Analysis

Multiple linear regressions of character vectors of each species on that of the outgroup (Rhinolophidae) revealed that the portion of the vector variance accounted for by the outgroup ranged from 79.6% *(Coelops robinsoni)* to 99.4% *(Hipposideros galeritus)* (see Table 2.1). Thus, the maximum-likelihood analyses were performed on residuals vectors representing from 20.4% to 0.6% of the original variance in the data from each species.

The majority consensus tree, computed from 50 original cladograms that were produced by changing the order of input taxa, indicates the existence of six relatively stable groups within the family (Figure 2.1): two of these are monotypic, two are characterized by 3–4 species, and two comprise as many as 24–25 taxa. The monotypic groups are composed of the Philippine species *Hipposideros pygmaeus* and the Australasian *Aselliscus tricuspidatus*. Within the multispecies clusters, the first one contains four small taxa (forearm length, <50 mm) from the genus *Hipposideros*, which are limited in their present distribution to New

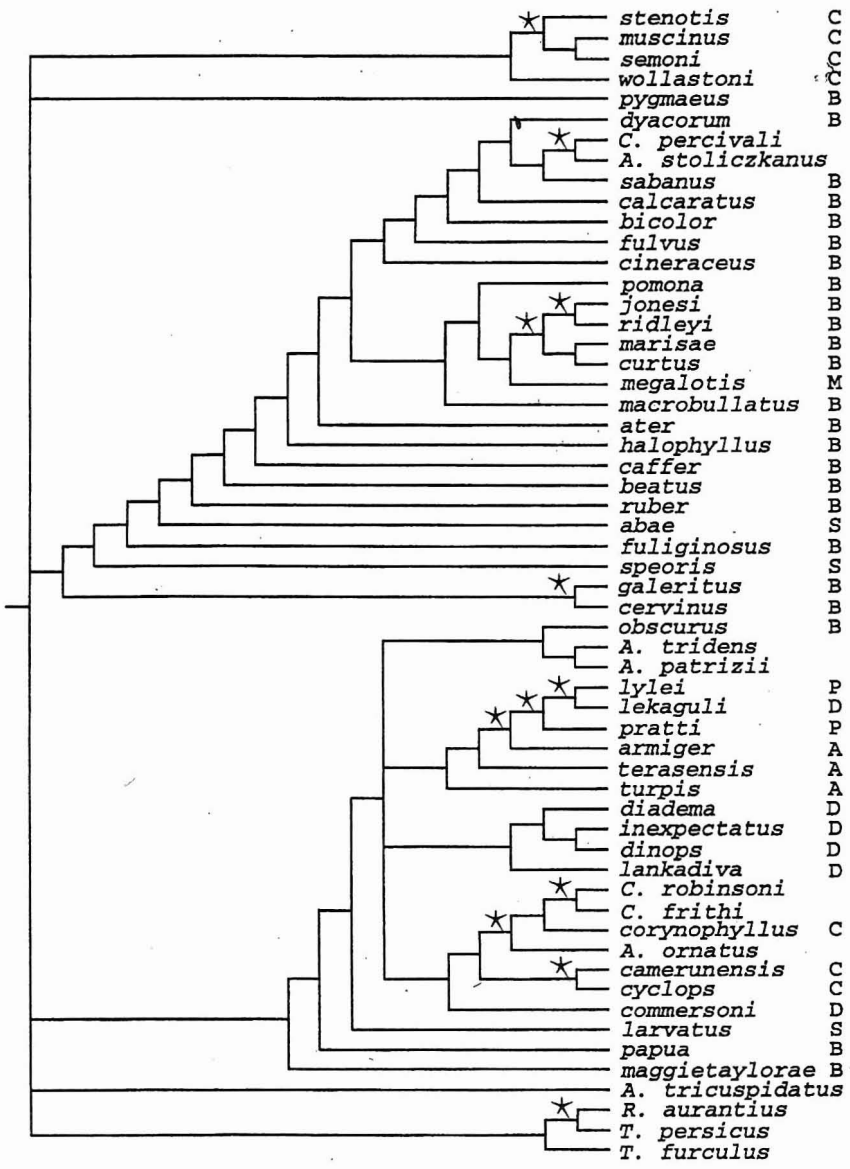

Figure 2.1. Majority consensus cladogram from 50 maximum-likelihood analyses of common-part-removed continuous-state data. Stars mark the taxonomic groupings that appear in 95% or more of the trees. Letters that follow taxon names denote species-group membership according to Hill (1963) and Koopman (1994): A, *armiger;* B, *bicolor;* C, *cyclops;* D, *diadema;* M, *megalotis;* P, *pratti;* S, *speoris.*

Guinea or northern Australia. The next two assemblages are formed by both *Hipposideros* and non-*Hipposideros* species from different regions of the Old World. Interestingly, all *Hipposideros* occurring in the first of these assemblages are characterized by small or medium forearm lengths, which frequently are less than 50 mm and almost never exceed 66 mm (*H. fuliginosus*, 56–64 mm; *H. abae*, 55–66 mm). The second assemblage is dominated by large and medium bats such as *H. pratti* (forearm length, 81–89 mm), *H. inexpectatus* (100–101 mm), *H. dinops* (93–97 mm), and *H. commersoni* (77–115 mm). The only exception is the small *H. obscurus* (40–52 mm) from the Philippines. The last polytypic cluster is formed by the Australian species *Rhinonycteris aurantius*, the Malagasy *Triaenops furculus*, and the primarily African *T. persicus*. All three taxa have similar noseleaf structure and greatly expanded zygoma.

Size-Free Analysis

The first principal component of $\log_e$-transformed morphometric data explains 89.8% of the variation, and all characters have high positive loadings on this component (see Table 2.2). The second through fourth components explain 3.1%, 1.5%, and 1.1%, respectively; each of the remaining components account for less than 1.0% of the variance. After removal of the first-component projections, the maximum-likelihood analysis was conducted on vectors from the remaining 44 components.

The majority consensus tree based on 50 size-free cladograms indicates very few groups that maintain stable structure under reordering of taxa in the data set (Figure 2.2). A few groups contain pairs of species morphologically similar to each other (e.g., *H. camerunensis* and *H. cyclops;*

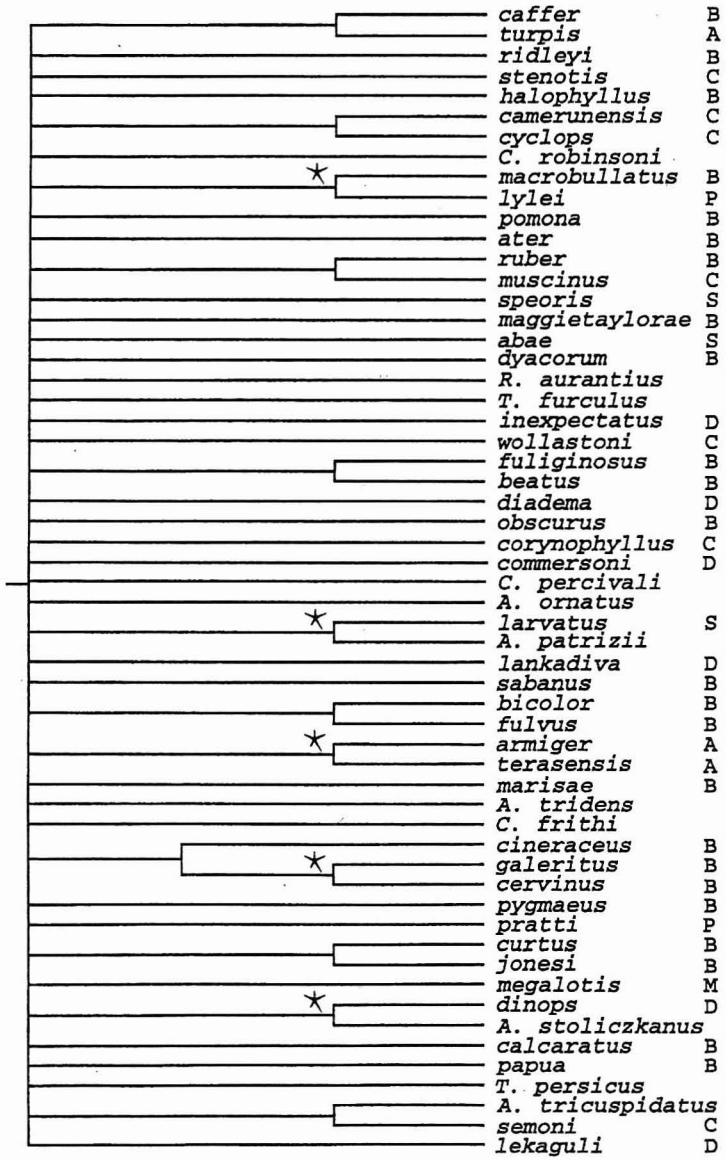

Figure 2.2. Majority consensus cladogram from 50 maximum-likelihood analyses of size-free continuous-state data. Stars mark the taxonomic groupings that appear in 95% or more of the trees. Letters that follow taxon names denote species-group membership according to Hill (1963) and Koopman (1994): A, *armiger;* B, *bicolor;* C, *cyclops;* D, *diadema;* M, *megalotis;* P, *pratti;* S, *speoris.*

and *H. galeritus* and *H. cervinus*). The majority, however, show no clear connections, even in the case of clusters with the 95% repeatability of branches (e.g., *H. macrobullatus* and *H. lylei;* and *H. dinops* and *A. stoliczkanus*).

Parsimony Analysis of Discrete-State Characters

The branch-and-bound algorithm gave 31,286 most-parsimonious trees with length of 99, consistency index of 0.32, and retention index of 0.69. In general, a low consistency index indicates that the data matrix does not "fit" the tree well (i.e., contains much homoplasy). A fairly good retention index value suggests, however, that many of the characters used are only partly homoplasious and that their transformation series show some synapomorphy for the particular tree topology. This determination is reflected in the relative stability of several clades present in the majority consensus tree, albeit this stability was exhibited mainly at the top of the tree. The affinities of the basal clades are less likely to be consistent, and it seems that at least four species could be treated as basal taxa: *Hipposideros bicolor, H. fulvus, H. semoni,* and *H. muscinus* (Figure 2.3). These hipposiderids differ from their hypothetical ancestor in that the center of the posterior border of hard palate is anterior to the posterior curvature of the palate bone (character 9) or is spiculated (character 10) (but see *H. muscinus*), and that metacarpal IV is longer than metacarpal V (character 29) (Appendix 2.2). In fact, the latter character is a synapomorphic feature of all the taxa studied, although it has been reversed in the two *Coelops* species and *H. corynophyllus.*

Above the four basal taxa, a trichotomy is formed from

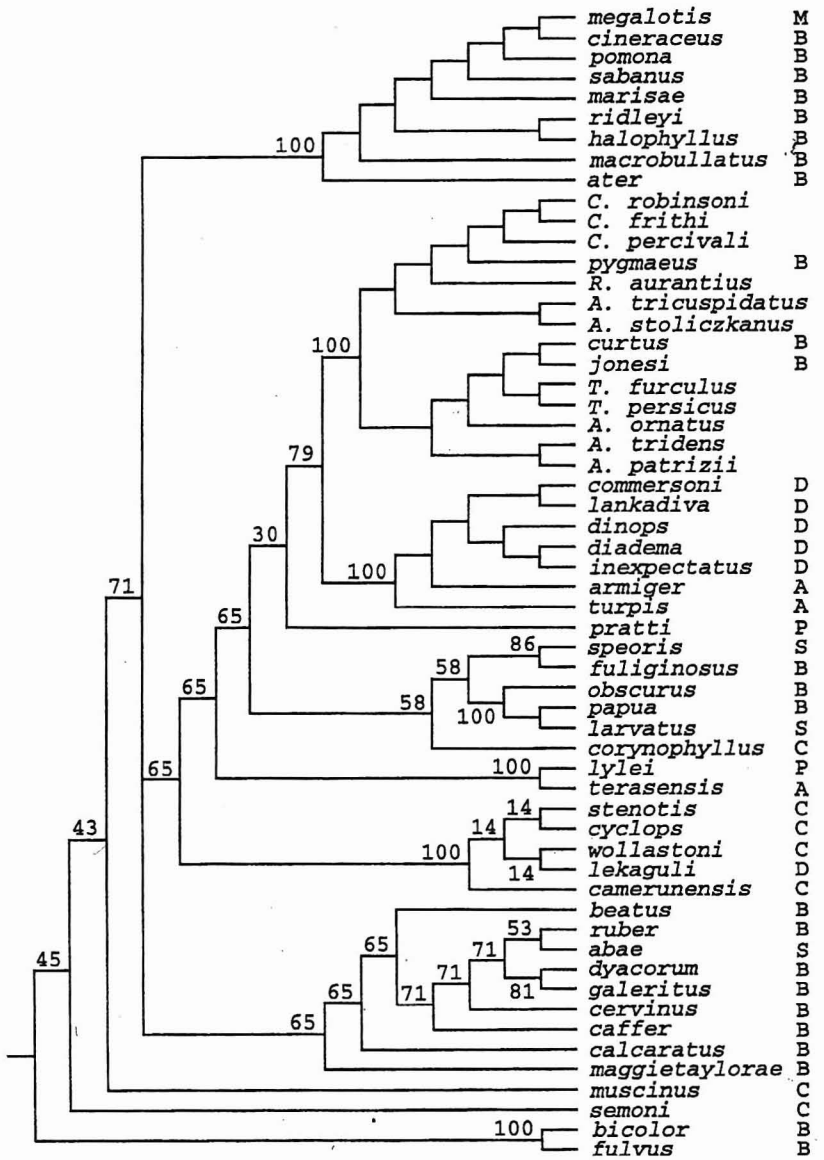

Figure 2.3. Nelson-like consensus cladogram from parsimony analysis of discrete-state data. Numbers at the forks indicate the percentage of times that the group consisting of the species which are to the right of that fork occurred among the 31,286 trees. Letters that follow taxon names denote species-group membership according to Hill (1963) and Koopman (1994): A, *armiger;* B, *bicolor;* C, *cyclops;* D, *diadema;* M, *megalotis;* P, *pratti;* S, *speoris.*

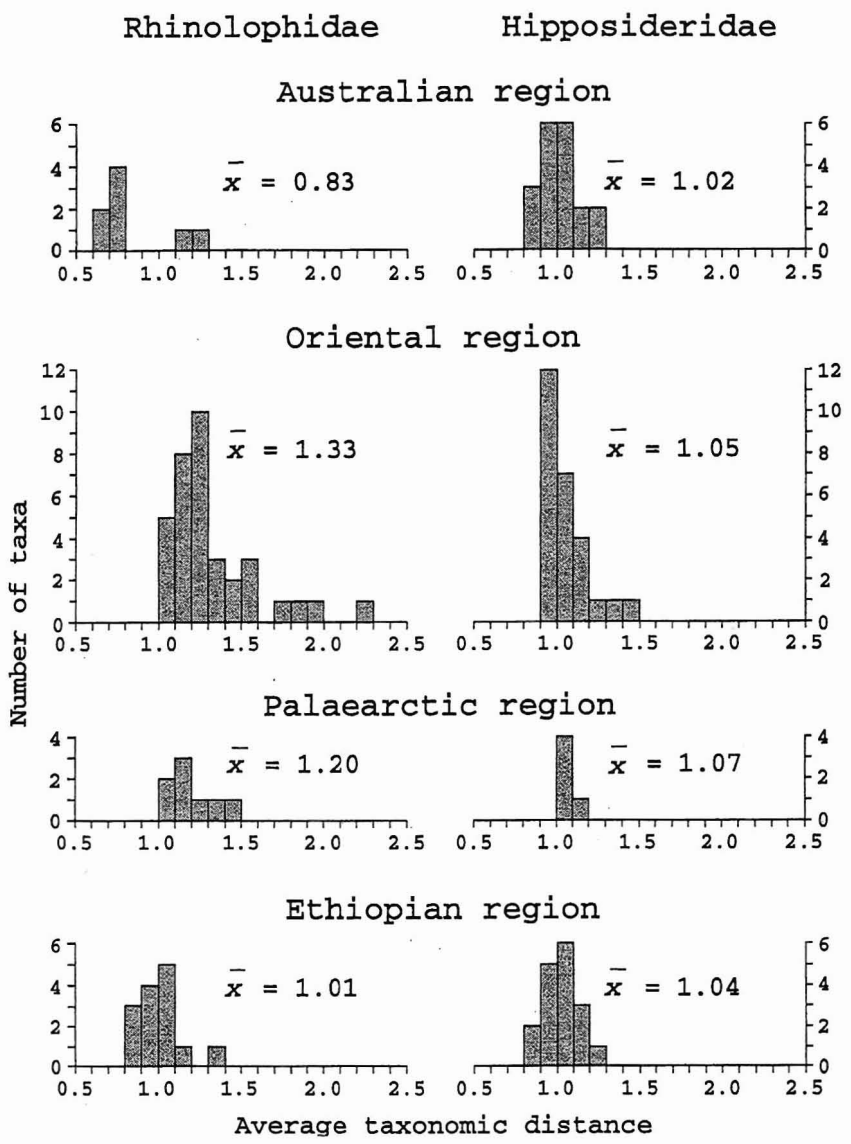

Figure 2.4. Distribution of average taxonomic distances among rhinolophid faunas (Bogdanowicz 1992) and hipposiderid faunas (this study) in four zoogeographic regions. $\bar{x}$ = overall mean taxonomic distance.

three polytypic lineages, one of which (upper lineage in Figure 2.3) can be found in all original trees. This clade comprises nine fairly small Asian and African species (forearm length, ≤48 mm), including large-eared *H. megalotis* from Kenya and Ethiopia. These species are closely related chiefly because they have one or both of the following features: a cranium that is relatively broad across the mastoids (character 4) and a foramen ovale of medium size (character 11). Both characters are partly homoplasious, and the latter especially shows strong parallelism with the second lineage (largest, central lineage), grouping all the remaining clades that are common to all competing trees. The other characteristic feature of this lineage is the presence of both *Hipposideros* and non-*Hipposideros* taxa and sister-group relationships of large hipposiderid bats (e.g., *H. commersoni, H. lankadiva, H. dinops,* and *H. inexpectatus*) and genera other than *Hipposideros.* Within the third lineage, relationships are not stable and several different tree topologies may exist (see Figure 2.3).

Morphological Dispersion and Origin of the Hipposideridae

For hipposiderids from the Ethiopian, Palaearctic, Oriental, and Australian regions, the average taxonomic distance values range from 1.02 to 1.07 (Figure 2.4) and the differences among the four faunas are not statistically significant (Kruskall–Wallis *H*-test, $\alpha = 0.05$). Pairwise comparisons also indicate that none of the studied faunas is more dispersed than another, although a nearly significant difference was observed between the Palaearctic and Australian faunas (Mann–Whitney *U*-test, $p = 0.051$), with the Palaearctic fauna being more dispersed morphologically.

In contrast, the distribution of average values is different

in different faunas. The Ethiopian and Australian regions are characterized by values more or less symmetrically distributed (skewness, 0.25 and 0.97, respectively), whereas those distributions in the Oriental and Palaearctic regions are skewed to the right (skewness, 1.52 and 1.88, respectively). These results suggest that the Oriental and Palaearctic faunas are composed of a majority of species that morphologically are close to their nearest neighbor. The most distinctive species is *Coelops robinsoni* (average taxonomic distance, 1.41) from the Oriental region, which together with *C. frithi* can easily be identified by the presence of a rudimentary tail and unusually short ears.

Discussion

Phylogenetic Relationships among Hipposiderids and Monophyly of the Genus *Hipposideros*

For the two metrical data sets used in this study, the transformation to remove the common part resulted in significantly higher stability of clades than did the transformation to remove size. The relationships suggested by the common-part-removed cladogram were more or less in good agreement with Hill's (1963) arrangements of *Hipposideros* taxa, grouping the majority of bats from the *bicolor* group into one clade and those from *diadema, pratti,* and *armiger* into the other (see Figure 2.1). This was not the case with the size-free majority consensus tree (see Figure 2.2), where even the clades with the highest repeatability frequently contained taxa without clear phylogenetic connections.

Interestingly, evolutionary affinities within the sister-family Rhinolophidae were also better explained by the common-part-removed cladogram than by the size-free cladogram (Bogdanowicz and Owen 1992). Wood (1983) reached similar conclusions, although about phenetic relationships, in his studies of storks (Ciconiidae) and cranes (Gruidae). In combination, these studies suggested that the use of the common-part-removed method may be applicable to the phylogenetic classifications of at least those vertebrates, such as bats and birds, that exhibit determinate growth.

The discrete-state consensus cladogram (see Figure 2.3) did not corroborate current systematic arrangements, and several taxa traditionally thought to be close systematically, such as those from the *bicolor* group, occurred in different clades; this may have resulted from a lack of sufficient material. A low character-to-taxon ratio (30:57) and the absence of some data (see Appendix 2.2) reduce the support for clades that include relatively incomplete taxa. On the other hand, the obtained consistency index values of original most-parsimonious trees, given the large number of taxa in the analysis, are only slightly less than the expected value (0.32 versus 0.34). Missing data, however, may also mask the presence of homoplasy and give higher consistency index values for matrices, with many cells scored as "?" (Sanderson and Donoghue 1989).

Despite these possible limitations, the consensus cladograms derived from the common-part-removed and discrete-state matrices have several features in common. First, both confirm close phylogenetic relationships between members of the *diadema* and *armiger* groups (Hill 1963). Second, the three species from the *speoris* group are much like certain species from the *bicolor* group. In our opinion, the taxonomic status of both groups needs to be redefined and revised (see also Kock and Bhat 1994). Third, large-eared *H. (Syndesmotis) megalotis* of the *megalotis* group, which is believed to be a single living descendant of the middle Miocene *Syndesmotis* lineage (Legendre 1982), constitutes a clade together with some bats of the *bicolor* group (see Figures 2.1 and 2.3) belonging to the subgenus *Hipposideros.* Such a phylogenetic position of *H. megalotis* contradicts both its subgeneric and its supraspecific group validity (see Hill 1963; Legendre 1982). Fourth, primarily African *Asellia* species and Southeast Asian *Coelops* species, as well as *Anthops ornatus* from the Solomon Islands, consistently occur within the clades composed of the *Hipposideros* taxa. In our opinion, this suggests that the genus *Hipposideros* does not comprise all the descendants of an ancestor and most probably should be treated as a paraphyletic group.

On the basis of fossil evidence, Legendre (1982) noted that species of the extinct subgenus *Hipposideros (Pseudorhinolophus)* are morphologically similar to some large Recent taxa, such as *H. armiger, H. diadema,* and *H. commersoni,* and could be ancestral to *Asellia* (see also Sigé 1968). Both consensus cladograms (see Figures 2.1 and 2.3) may support this hypothesis.

The status of the other non-*Hipposideros* genera seems to be more complicated. *Rhinonycteris aurantius* is thought to be closely related to *Brachipposideros nooraleebus* from the middle Miocene deposits from Riversleigh, Australia (Sigé et al. 1982; Hand 1993; Archer et al. 1994). The common-part-removed and discrete-state cladograms do not contradict this interpretation, although the position of *Rhinonycteris* in the second of these cladograms may indicate its closer relationships with large rather than small *Hipposideros* species. In the light of the microcomplement fixation transferrin data, however, *Rhinonycteris* is outside both the *Hipposideros* and *Rhinolophus* genera (Pierson 1986). Its distance from these genera (103 and 110 units, respectively) was substantially greater than the distance between them (74 and 84 units). *Aselliscus* was much closer (44 versus 81

units) to *Rhinolophus* than to *Hipposideros,* and about the same distance from *Hipposideros* as was *Rhinolophus* (81 and 84 units, respectively). Evidently, the results of morphological and immunological data may not be comparable at all levels in the phylogeny. Optimum resolution at different evolutionary levels by albumin, electrophoretic, chromosomal, and morphological characters was shown by Arnold et al. (1982) in a study on phyllostomoid bats.

Morphological Dispersion, Cladograms, and Center of Origin

Findley (1976) reasoned that older bat faunas are phenotypically more diverse. Our analysis indicated that, unlike rhinolophids (Bogdanowicz and Owen 1992), hipposiderids have no significant differences in morphological dispersion among the Ethiopian, Palaearctic, Oriental, and Australian regions (see Figure 2.4). Our results suggest (albeit weakly) that the Palaearctic fauna might be older than the Australian fauna (Mann–Whitney *U*-test, $p = 0.051$), and this hypothesis, while considering the age of fossil taxa, agrees with palaeontological findings.

The maximum-likelihood cladograms do not give any constructive suggestion about the center of origin for the family, because at least six clades might be ancestral (see Figures 2.1 and 2.2). On the other hand, the most basal hipposiderids on the consensus cladogram derived from the discrete-state data (Figure 2.3) are recently known from Afghanistan, Pakistan, India, and Sri Lanka *(H. fulvus),* and from Thailand, Malaysia, Indonesia, and the Philippines *(H. bicolor).* The next two basal species *(H. semoni* and *H. muscinus)* are limited in their present distribution to New Guinea or northeastern Queensland in Australia (Corbet and Hill 1992; Koopman 1994). However, it is generally assumed that Australia was colonized by bats migrating from Asia rather than from South America (Hamilton-Smith 1975; Flannery 1989; Hand et al. 1994), although their appearance in Australia predates the final breakup of Gondwana (Hand et al. 1994). The arrival of hipposiderids into New Guinea most probably occurred during the Miocene (*Hipposideros* spp.) and Pliocene *(Aselliscus tricuspidatus)* (Flannery 1990).

To date it has been generally accepted that the family originated somewhere in the Old World tropics, probably in Africa or Asia (Koopman 1970; Sigé 1991), and only recently Hand et al. (1994) suggested, although indirectly, that it may have evolved in the Southern Hemisphere. The Tertiary karstic fissure-fills of western Europe show that from the late Eocene to at least the middle Oligocene, hipposiderids were the most diverse and numerous group of the cave-dwelling bats and that their distribution in the past was wider than it is today (Hand 1984; Sevilla 1990). Their oldest remains are known from the late middle Eocene of Europe (e.g., Sigé and Legendre 1983; Sigé 1991). Based on fossil evidence, hipposiderids were present in Arabo-Africa and Australia by the early and late Oligocene (Archer et al. 1994; Sigé et al. 1994), respectively. In contrast, their known fossil remains in the Oriental region are very few and relatively young, dating back only to the Neogene (Hand 1984, p. 883; K. F. Koopman, in litt.). In our opinion, however, the lack of older Oriental material should provisionally be treated as an artifactual product of the general unavailability of well-examined fossil material from this region, because we find support from the neontological data to indicate that the Hipposideridae, like their sister-family Rhinolophidae (Bogdanowicz and Owen 1992), most probably originated in Asia, not in Africa (but see Sigé 1991). This hypothesis of origin would also be consistent with the paleoclimatic evidence of tropical rainforest development in Southeast Asia during the Tertiary (Heaney 1991), as it is generally agreed that the family Hipposideridae would have developed and radiated in such conditions (B. Sigé, in litt.).

Karyology and Phylogenetic Relationships

As far as we are aware, karyotypes of 22 hipposiderid species have been described (Table 2.3). Six diploid chromosome numbers have been encountered for these species, with only two within the genus *Hipposideros* ($2n = 32, 52$).

It is very important for phylogenetic considerations to determine the mode and direction of karyotypic change in the family studied. First, at the level of nondifferentially stained karyotypes, the genus *Hipposideros* shows considerable karyotypic conservatism, and for all but one species, $2n = 32$ and the number of autosomal arms (FN) = 60. Rautenbach et al. (1993) suggested that the chromosomal complement of *H. commersoni* ($2n = 52$, FN = probably 60) may have evolved from the most common hipposiderid state by 10 centric fissions, producing change in diploid number but not in fundamental number. On the basis of data on the G-banded chromosomes, Sreepada et al. (1993) proposed that the ancestral lineage of *Hipposideros* derived from a rhinolophoid ancestor whose karyotype was similar to that of *R. luctus* ($2n = 32$, FN = 60; Naidu and Gururaj 1984; Harada et al. 1985b; Hood et al. 1988). However, direct comparison of the banding pattern in chromosomes of *R. luctus* and *Hipposideros* spp. is not available. Homology of these karyotypes is thus not clear, and the arm combination in metacentric autosomes may differ.

Second, karyological data suggest that the autosomes for the ancestral karyotype in the sister-family Rhinolophidae contained all acrocentric elements with $2n = 62$ and FN =

Table 2.3
Synopsis of Karyotypes of Hipposiderids

Species	2*n*	FN	X	Y	Reference
Asellia tridens	50	62	SM	A	Baker et al. 1974
Aselliscus stoliczkanus	30	56	SM	A	Harada et al. 1985a
Cloeotis percivali	40	?	?	?	Rautenbach et al. 1993
Coelops frithi	30	56	ST	ST	Andō et al. 1980
Hipposideros armiger	32	60	SM	ST	Hood et al. 1988; Qumsiyeh et al. 1988
Hipposideros ater	32	60	SM	A	Ray-Chaudhuri et al. 1971; Sreepada et al. 1993
Hipposideros bicolor	32	60?	?	?	Ray-Chaudhuri and Pathak 1966
Hipposideros caffer	32	60	ST	A	Peterson and Nagorsen 1975
	32	60	SM	A	Rautenbach et al. 1993
	32	60	?	?	Dulić and Mutere 1974
Hipposideros cervinus	32	60	SM	A	Harada and Kobayashi 1980
Hipposideros cineraceus	32	60	SM	A	Sreepada et al. 1993
Hipposideros commersoni	52	60?	?	?	Rautenbach et al. 1993
Hipposideros diadema	32	60	SM	A	Harada and Kobayashi 1980
Hipposideros fulvus	32	60	SM	A	Ray-Chaudhuri et al. 1971; Harada et al. 1985a; Hood et al. 1988
	32	60	M	A	Sreepada et al. 1993
	32	60	M	ST	Handa and Kaur 1980
Hipposideros hypophyllus	32	60	M	A	Sreepada et al. 1993
Hipposideros lankadiva	32	60	M	A	Sreepada et al. 1993
	32	60	M	ST	Handa and Kaur 1980
Hipposideros larvatus	32	60	SM	ST	Harada et al. 1982; Hood et al. 1988
Hipposideros lekaguli	32	60	SM	ST	Harada et al. 1982; Hood et al. 1988
Hipposideros pratti	32	60	M	ST	Zhang 1985
Hipposideros speoris	32	60	ST	A	Sreepada et al. 1993
	32	60?	SM	A	Dulić 1984 (Figure 3)
	32	60	SM	ST	Handa and Kaur 1980
Hipposideros terasensis	32	60	ST	A	Andō et al. 1980
Hipposideros turpis	32	60	ST	A	Andō et al. 1980
Triaenops persicus	36	60	M	ST	Dulić and Mutere 1977

Notes: 2*n*, diploid number of chromosomes; FN, total number of autosomal arms; X, Y, sex chromosomes (states: A, acrocentric; M, metacentric; SM, submetacentric; ST, subtelocentric). The karyotypes of *Hipposideros cervinus*, *H. hypophyllus*, and *H. terasensis* were originally described as those of *H. galeritus labuanensis*, *H. pomona*, and *H. armiger terasensis*, respectively (reviewed by Jenkins and Hill 1981; Yoshiyuki 1991; Kock and Bhat 1994).

60 (summarized by Zima et al. 1992; see also Bogdanowicz and Owen 1992). This interpretation also is supported by phylogenetic analyses of morphological characters (Bogdanowicz and Owen 1992). An acrocentric composition of the primitive karyotype, and the trend toward low diploid chromosome numbers, have also been suggested for the families Phyllostomidae and Vespertilionidae (Baker and Bickham 1980). Third, a newly described fossil genus *Vaylatsia*, although a member of the Hipposideridae, probably represents the stem group of *Rhinolophus* (Sigé 1990).

In light of these considerations, it seems that the autosomes of the common ancestor of Rhinolophidae and Hipposideridae consisted of all acrocentrics rather than metacentrics and that the trend was toward low, rather than high, diploid numbers. A comparison between the G-banded chromosomes of *R. acuminatus* and *H. armiger* also indicated that some non-Robertsonian processes must have occurred during the evolution from the ancestral karyotype to the karyotypes we find today (Qumsiyeh et al. 1988). This assessment does not contradict phylogenetic relationships suggested by the common-part-removed cladogram and seems to be in partial agreement with the positions of mainly non-*Hipposideros* species shown in the discrete-state cladogram. Their karyotypes have probably undergone extensive Robertsonian and non-Robertsonian changes, which resulted in the variable number of chromosomes (2*n* = 30–50) and autosomal arms (FN = 56–62) (see Table 2.3).

Conclusions

Several standard and novel analyses of a morphological data set, supplemented with karyotypic information, were used in search of a robust hypothesis for the phylogeny and

the center of origin of the bat family Hipposideridae. The results suggest that phylogenetic affinities among Recent species are not expressed accurately by current systematic arrangements based on Hill's (1963) supraspecific groupings and that the genus *Hipposideros* might be a paraphyletic taxon. Morphological dispersion analysis failed to reveal any significant differences in morphological diversification among hipposiderid faunas from four zoogeographic regions, and no center of origin could be inferred from the analyses of phenetic data. From phylogenetic evidence, however, it appears that the family most probably originated somewhere in the Oriental region. Our analyses also suggest that the common ancestor of the sister-families Rhinolophidae and Hipposideridae had all acrocentric rather than metacentric autosomes, and that these families independently followed a pattern of Robertsonian fusions, with the result that low diploid numbers are the derived condition in both lineages.

The phylogenetic relationships suggested by this study (Figures 2.1 and 2.3) are supported by metric and nonmetric morphological data and should be considered tentative, as working hypotheses. Future study must adopt the total-evidence approach, combining morphological, genetic, and biochemical character sets and determining the most-parsimonious outcome of the pooled matrix. We still have a long way to go in the field of hipposiderid phylogeny, but, like Theseus in the Minotaur's labyrinth, we have few landmarks to guide us.

Appendix 2.1. The 30 Characters in the Parsimony Analysis of the Hipposideridae

1. Hornlike crest in middle of dorsal part of premaxillae: (0) absent; (1) present.
2. Location of greatest neurocranial breadth, dorsal view: (0) anterior cranium or middle of cranium; (1) posterior cranium.
3. Position of braincase, excluding sagittal crest: (0) evidently higher than rostrum; (1) almost as high as or lower than rostrum.
4. Distance between mastoids: (0) less than or equal to zygomatic breadth; (1) greater than zygomatic breadth.
5. Zygoma, lateral view: (0) not expanded at all to moderately expanded; (1) expanded into a wide plate.
6. Anterior end of sagittal crest: (0) extends to interorbital constriction; (1) extends past interorbital constriction.
7. Lambdoidal crest: (0) absent or weak; (1) extremely well-developed.
8. Perforations behind nasal swellings: (0) zero to five foramina present; (1) more than five foramina present.
9. Location of central portion of posterior border of hard palate, ventral view: (0) behind or at the level of posterior curvature of palate bone; (1) anterior to posterior curvature of palate bone.
10. Posterior nasal spine (i.e., spicule at the center of posterior edge of hard palate): (0) absent or inconspicuous; (1) well-developed.
11. Foramen ovale: (0) small; (1) medium—about half the size of glenoid fossa; (2) almost as large as glenoid fossa. The linear character transformation is hypothesized to be $0 > 1 > 2$.
12. Type of cochlea: (0) phanaerocochlear; (1) cryptocochlear. This character and its states correspond to those distinguished by Novacek (1991), although some of our findings differ; we found both states present in more species, and a state different from that reported by Novacek (1991) for several species.
13. Least basioccipital width: (0) less than or equal to the least width of the sphenoidal bridge; (1) greater than the least width of the sphenoidal bridge.
14. Foramen magnum: (0) elliptical; (1) oval.
15. Shape of hamular process of the pterygoids, lateral view: (0) strongly notched; (1) weakly or not at all indented.
16. Size of hamular process of the pterygoids: (0) long, practically reaching glenoid fossa; (1) short.
17. Anterior edge of the ascending mandibular ramus: (0) posterior to or at the middle of last upper molar; (1) anterior to the middle of last upper molar.
18. Position of mental foramen, lateral view: (0) anterior to or in the middle of first premolar; (1) posterior to the middle of first premolar.
19. Bone connection between angular and condyloid processes, lateral view: (0) strongly notched; (1) shallow.
20. Posterior cusp on upper canines (usually one-quarter to one-half the height of canine): (0) absent; (1) present.
21. Heel of second upper molar: (0) well-developed; (1) inconspicuous.
22. Shape of third upper molar, buccal view: (0) pentagonal; (1) triangular.
23. Anterior segment (parastyle–paracone–mesostyle triangle) of third upper molar, occlusal view: (0) almost as large as that of the second upper molar; (1) much smaller than that of the second upper molar.
24. Lobes on the lower inner incisors: (0) three full lobes; (1) two full lobes plus a third, rudimentary lobe; (2) only two lobes. The linear character transformation is hypothesized to be $0 > 1 > 2$.
25. Diastema between first lower incisors: (0) absent; (1) present.
26. Diastema between the last lower incisors and lower canines: (0) absent; (1) present.
27. Horizontal ribs on outer parts of ears: (0) present; (1) absent.
28. Third metacarpal: (0) shorter than fifth metacarpal; (1) longer than fifth metacarpal.
29. Fourth metacarpal: (0) shorter than fifth metacarpal; (1) longer than fifth metacarpal.
30. Tail: (0) well-developed; (1) rudimentary.

Appendix 2.2.
Distribution of States for the 30 Characters within Taxa of the Family Hipposideridae

Characters and their states are as defined in Appendix 2.1. For all characters, state 0 is plesiomorphic, and states 1 and 2 are apomorphic. In the data matrix shown here, the letter "B" indicates that both states 0 and 1 are present (this was coded as "?" in Hennig86), and a question mark means that the state is unknown.

	Character																														
Taxon	1	2	3	4	5	6	7	8	9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anthops ornatus	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1
Asellia patrizii	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	1	1	0
Asellia tridens	0	0	1	0	0	1	0	1	1	0	0	B	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	1	0
Aselliscus stoliczkanus	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	1	1	0
Aselliscus tricuspidatus	0	0	0	0	0	0	0	0	0	0	1	0	0	B	0	0	0	0	1	1	0	0	0	0	0	B	0	1	1	0
Cloeotis percivali	1	0	0	0	0	0	0	1	0	1	2	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0	1	1	1	0
Coelops frithi	0	1	0	0	0	0	0	1	1	B	2	0	0	1	0	0	0	B	0	1	0	0	0	0	0	1	1	0	0	1
Coelops robinsoni	0	1	0	0	0	0	0	1	1	1	2	0	0	B	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	1
Hipposideros abae	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Hipposideros armiger	0	0	0	0	0	0	1	0	1	0	0	B	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Hipposideros ater	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros beatus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	?	0	0	0	1	0	1	0	0	0	0	0	1	1	0
Hipposideros bicolor	0	0	0	0	0	0	0	0	1	0	0	0	B	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros caffer	0	0	0	1	0	0	0	0	0	0	0	B	1	0	0	0	0	0	0	1	0	0	0	0	0	B	0	1	1	0
Hipposideros calcaratus	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Hipposideros camerunensis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B	0	0	1	1	0
Hipposideros cervinus	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Hipposideros cineraceus	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros commersoni	0	0	1	0	0	1	1	0	1	0	0	B	0	0	0	0	B	0	0	0	0	1	0	0	B	0	0	1	1	0
Hipposideros corynophyllus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0
Hipposideros curtus	0	0	0	1	0	0	0	1	1	1	0	B	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0
Hipposideros cyclops	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0
Hipposideros diadema	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0
Hipposideros dinops	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	0	B	0	0	0	0	0	0	1	0	0	0	1	1	0
Hipposideros dyacorum	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Hipposideros fuliginosus	0	0	0	0	0	0	0	0	1	0	0	B	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0
Hipposideros fulvus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros galeritus	0	0	0	0	0	0	0	0	1	0	0	0	B	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Hipposideros halophyllus	0	0	0	1	0	0	0	0	1	0	2	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Hipposideros inexpectatus	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0
Hipposideros jonesi	0	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0
Hipposideros lankadiva	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Hipposideros larvatus	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	0
Hipposideros lekaguli	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Hipposideros lylei	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Hipposideros macrobullatus	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros maggietaylorae	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Hipposideros marisae	0	0	0	1	0	0	0	0	1	1	1	0	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros megalotis	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	B	0	0	1	0
Hipposideros muscinus	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Taxon *(continued)*	Character																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Hipposideros obscurus	0	0	0	0	0	0	0	0	0	1	0	B	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0
Hipposideros papua	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	B	0	0	1	0	1	0	0	0	B	0	1	1	0
Hipposideros pomona	0	0	0	1	0	0	0	0	1	0	1	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros pratti	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Hipposideros pygmaeus	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Hipposideros ridleyi	0	0	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros ruber	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Hipposideros sabanus	0	0	0	0	0	0	0	1	1	0	1	0	1	0	?	?	0	B	0	0	0	1	0	0	0	0	0	0	1	0
Hipposideros semoni	0	0	0	0	0	0	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Hipposideros speoris	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0
Hipposideros stenotis	0	0	0	0	0	0	0	0	?	1	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Hipposideros terasensis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B	0	0	0	0	0	1	1	0
Hipposideros turpis	0	0	0	0	0	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0
Hipposideros wollastoni	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Rhinonycteris aurantius	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0
Triaenops furculus	1	0	1	0	1	B	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	1	0
Triaenops persicus	1	0	1	0	1	B	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	1	1	0

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Literature Cited

Andō, K., T. Tagawa, and T. A. Uchida. 1980. Karyotypes of Taiwanese and Japanese bats belonging to the families Rhinolophidae and Hipposideridae. Cytologia (Tokyo) 45:423–432.

Archer, M., S. J. Hand, and H. Godthelp. 1994. Riversleigh. The Story of Animals in Ancient Rainforests of Inland Australia. Reed Books, Sydney.

Arnold, M. L., R. L. Honeycutt, R. J. Baker, V. M. Sarich, and J. K. Jones, Jr. 1982. Resolving a phylogeny with multiple data sets: A systematic study of phyllostomoid bats. Occasional Papers of the Museum, Texas Tech University 77:1–15.

Baker, R. J., and J. W. Bickham. 1980. Karyotypic evolution in bats: Evidence of extensive and conservative chromosomal evolution in closely related taxa. Systematic Zoology 29:239–253.

Baker, R. J., B. L. Davis, R. G. Jordan, and A. Binous. 1974. Karyotypic and morphometric studies of Tunisian mammals: Bats. Mammalia 38:695–710.

Bogdanowicz, W. 1992. Phenetic relationships among bats of the family Rhinolophidae. Acta Theriologica 37:213–240.

Bogdanowicz, W., and R. D. Owen. 1992. Phylogenetic analyses of the bat family Rhinolophidae. Zeitschrift für Zoologische Systematik und Evolutionsforschung 30:142–160.

Corbet, G. B., and J. E. Hill. 1991. A World List of Mammalian Species, 3rd Ed. Natural History Museum Publications and Oxford University Press, London.

Corbet, G. B., and J. E. Hill. 1992. The Mammals of the Indomalayan Region. Oxford University Press, Oxford.

Dulić, B. 1984. Chromosomes of four Indian species of Microchi-

roptera. *In* Proceedings of the Sixth International Bat Research Conference, E. E. Okon and A. E. Caxton-Martins, eds., pp. 25–37. University of Ife Press, Ile-Ife.

Dulić, B., and F. A. Mutere. 1974. The chromosomes of two bats from East Africa: *Rhinolophus clivosus* Cretzschmar, 1828 and *Hipposideros caffer* (Sundevall, 1846). Periodicum Biologorum 76:31–34.

Dulić, B., and F. A. Mutere. 1977. Chromosomes of some East African bats. Säugetierkundliche Mitteilungen 25:231–233.

Farris, J. S. 1988. Hennig86, version 1.5. Computer program and documentation. Port Jefferson Station, N.Y.

Felsenstein, J. 1981. Evolutionary trees from gene frequencies and quantitative characters: Finding maximum likelihood estimates. Evolution 35:1229–1242.

Felsenstein, J. 1993. PHYLIP (Phylogeny Inference Package), version 3.5p. Software and documentation. University of Washington, Seattle.

Findley, J. S. 1976. The structure of bat communities. American Naturalist 110:129–139.

Flannery, T. F. 1989. Origins of the Australo-Pacific land mammal fauna. Australian Zoological Reviews 1:15–24.

Flannery, T. F. 1990. Mammals of New Guinea. Robert Brown, Carina, Queensland, Australia.

Freeman, P. W. 1981. A multivariate study of the family Molossidae (Mammalia, Chiroptera): Morphology, ecology, evolution. Fieldiana Zoology 1316:1–173.

Hamilton-Smith, E. 1975. Gondwanaland and the Chiroptera. Journal of the Australian Mammal Society 1:382–383.

Hand, S. 1984. Bat beginnings and biogeography: A southern perspective. *In* Vertebrate Zoogeography and Evolution in Australia: Animals in Space and Time, M. Archer and G. Clayton, eds., pp. 853–904. Hesperian Press, Carlisle, Australia.

Hand, S. J. 1993. First skull of a species of *Hipposideros (Brachipposideros)* (Microchiroptera: Hipposideridae), from Australian Miocene sediments. Memoirs of the Queensland Museum 33:179–182.

Hand, S., M. Novacek, H. Godthelp, and M. Archer. 1994. First Eocene bat from Australia. Journal of Vertebrate Paleontology 14:375–381.

Handa, S. M., and S. Kaur. 1980. Chromosome studies on three species of *Hipposideros* (Hipposideridae: Chiroptera). Caryologia 33:537–549.

Harada, M., and T. Kobayashi. 1980. Studies on the small mammal fauna of Sabah, East Malaysia. II. Karyological analysis of some Sabahan mammals (Primates, Rodentia, Chiroptera). Contributions from the Biological Laboratory, Kyoto University 26: 83–95.

Harada, M., M. Minezawa, S. Takada, S. Yenbutra, P. Nunpakdee, and S. Ohtani. 1982. Karyological analysis of 12 species of bats from Thailand. Caryologia 35:269–278.

Harada, M., S. Yenbutra, K. Tsuchiya, and S. Takada. 1985a. Karyotypes of seven species of bats from Thailand (Chiroptera, Mammalia). Experientia (Basel) 41:1610–1611.

Harada, M., S. Yenbutra, T. H. Yoshida, and S. Takada. 1985b. Cytogenetical study of *Rhinolophus* bats (Chiroptera, Mammalia) from Thailand. Proceedings of the Japan Academy 61B: 455–458.

Heaney, L. R. 1991. A synopsis of climatic and vegetational change in Southeast Asia. Climatic Change 19:53–61.

Hendy, M. D., and D. Penny. 1982. Branch and bound algorithms to determine minimal evolutionary trees. Mathematical Biosciences 59:277–290.

Hill, J. E. 1963. A revision of the genus *Hipposideros*. Bulletin of the British Museum (Natural History) Zoology 11:1–129.

Hill, J. E. 1982. A review of the leaf-nosed bats *Rhinonycteris, Cloeotis,* and *Triaenops* (Chiroptera: Hipposideridae). Bonner Zoologische Beiträge 33:165–186.

Hood, C. S., D. A. Schlitter, J. I. Georgudaki, S. Yenbutra, and R. J. Baker. 1988. Chromosomal studies of bats (Mammalia: Chiroptera) from Thailand. Annals of Carnegie Museum 57:99–109.

Jenkins, P. D., and J. E. Hill. 1981. The status of *Hipposideros galeritus* Cantor, 1846 and *Hipposideros cervinus* (Gould, 1854) (Chiroptera: Hipposideridae). Bulletin of the British Museum (Natural History) Zoology 41:279–294.

Kock, D., and H. R. Bhat. 1994. *Hipposideros hypophyllus* n. sp. of the *H. bicolor* group from peninsular India (Mammalia: Chiroptera: Hipposideridae). Senckenbergiana Biologica 73:25–31.

Koopman, K. F. 1970. Zoogeography of bats. *In* About Bats: A Chiropteran Biology Symposium, B. H. Slaughter and D. W. Walton, eds., pp. 29–50. Southern Methodist University Press, Dallas.

Koopman, K. F. 1994. Chiroptera: Systematics. *In* Handbook of Zoology, Vol. 8. Mammalia, Part 60. de Gruyter, Berlin.

Legendre, S. 1982. Hipposideridae (Mammalia: Chiroptera) from the Mediterranean Middle and Late Neogene and evolution of the genera *Hipposideros* and *Asellia*. Journal of Vertebrate Paleontology 2:386–399.

Lincoln, R. J., G. A. Boxshall, and P. F. Clark. 1982. A Dictionary of Ecology, Evolution, and Systematics. Cambridge University Press, Cambridge.

Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. Systematic Zoology 33:83–103.

Naidu, K. N., and M. E. Gururaj. 1984. Karyotype of *Rhinolophus luctus*. Current Science (Bangalore) 53:825–826.

Norušis, M. J. 1993. SPSS for Windows, release 6.0. Software and documentation. SPSS, Inc., Chicago.

Nelson, G. 1979. Cladistic analysis and synthesis: Principles and definitions, with a historical note on Adanson's *Familles des Plantes* (1763–1764). Systematic Zoology 28:1–21.

Novacek, M. J. 1991. Aspects of the morphology of the cochlea in microchiropteran bats: An investigation of character transformation. Bulletin of the American Museum of Natural History 206:84–100.

Peterson, R. L., and D. W. Nagorsen. 1975. Chromosomes of fifteen species of bats (Chiroptera) from Kenya and Rhodesia. Life Sciences Occasional Papers, Royal Ontario Museum 27:1–14.

Pierson, E. D. 1986. Molecular systematics of the Microchiroptera: Higher taxon relationships and biogeography. Ph.D. dissertation, University of California, Berkeley.

Qumsiyeh, M. B., R. D. Owen, and R. K. Chesser. 1988. Differen-

tial rates of genic and chromosomal evolution in bats of the family Rhinolophidae. Genome 30:326–335.

Radinsky, L. 1967. Relative brain size: A new measure. Science 155:836–838.

Rautenbach, I. L. 1986. Karyotypical variation in southern African Rhinolophidae (Chiroptera) and non-geographic morphometric variation in *Rhinolophus denti* Thomas, 1904. Cimbebasia 8A:130–139.

Rautenbach, I. L., G. N. Bronner, and D. A. Schlitter. 1993. Karyotypic data and attendant systematic implications for the bats of southern Africa. Koedoe 36:87–104.

Ray-Chaudhuri, S. P., and S. Pathak. 1966. Studies on the chromosomes of bats: List of worked out Indian species of Chiroptera. Mammalian Chromosome Newsletter 22:206.

Ray-Chaudhuri, S. P., S. Pathak, and T. Sharma. 1971. Karyotypes of five Indian species of Microchiroptera. Caryologia 24:239–245.

Rohlf, F. J. 1993. NTSYS-pc: Numerical Taxonomy and Multivariate Analysis System, Version 1.80. Exeter Software, Setauket, N.Y.

Sanderson, M. J., and M. J. Donoghue. 1989. Patterns of variation in levels of homoplasy. Evolution 43:1781–1795.

Sevilla, P. 1990. Rhinolophoidea (Chiroptera, Mammalia) from the upper Oligocene of Carrascosa del Campo (central Spain). Geobios (Lyon) 23:173–188.

Sigé, B. 1968. Les chiroptères du Miocène inférieur de Bouzigues. I. Etude systématique. Palaeovertebrata 1:65–133.

Sigé, B. 1990. Nouveaux chiroptères de l'Oligocène moyen des phosphorites du Quercy, France. Comptes Rendus de l'Académie des Sciences, Paris, Série II 310:1131–1137.

Sigé, B. 1991. Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocène inférieur de Tunisie). Aspects biostratigraphique, biogéographique et paléoécologique de l'origine des chiroptères modernes. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 182:355–376.

Sigé, B., and S. Legendre. 1983. L'histoire des peuplements de chiroptères du basin méditerranéen: L'apport comparé des remplissages karstiques et des dépôts fluvio-lacustres. Mémoires de Biospéologie 10:209–225.

Sigé, B., S. J. Hand, and M. Archer. 1982. An Australian Miocene *Brachipposideros* (Mammalia, Chiroptera) related to Miocene representatives from France. Palaeovertebrata 12:149–171.

Sigé, B., H. Thomas, S. Sen, E. Gheerbrant, J. Roger, and Z. Al-Sulaimani. 1994. Les chiroptères de Taqah (Oligocène inférieur, Sultanat d'Oman). Premier inventaire systématique. Münchner Geowissenschaftliche Abhandlungen 26A:35–48.

Sreepada, K. S., K. N. Naidu, and M. E. Gururaj. 1993. Trends of karyotypic evolution in the genus *Hipposideros* (Chiroptera: Mammalia). Cytobios 75:49–57.

Tate, G. H. H. 1941. Results of the Archbold expeditions. No. 35. A review of the genus *Hipposideros* with special reference to Indo-Australian species. Bulletin of the American Museum of Natural History 78:353–371.

Wood, D. S. 1983. Character transformations in phenetic studies using continuous morphometric variables. Systematic Zoology 32:125–131.

Yoshiyuki, M. 1991. Taxonomic status of *Hipposideros terasensis* Kishida, 1924 from Taiwan (Chiroptera, Hipposideridae). Journal of the Mammalogical Society of Japan 16:27–35.

Zhang, W. 1985. A study on karyotypes of the bats *Tadarida teniotis insignis* Blyth and *Hipposideros pratti* Thomas. Acta Theriologica Sinica 5:189–193.

Zima, J., M. Volleth, I. Horáček, J. Cerveny, A. Cervená, K. Prucha, and M. Macholán. 1992. Comparative karyology of rhinolophid bats (Chiroptera: Rhinolophidae). *In* Prague Studies in Mammalogy, I. Horáček and V. Vohralík, eds., pp. 229–236. Charles University Press, Prague.