

A Phylogeny of the Neotropical Nectar-Feeding Bats (Chiroptera: Phyllostomidae) Based on Morphological and Molecular Data

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We present a phylogeny of 35 species of nectar-feeding bats based on 119 morphological characters: 62 from the skin, skull, and dentition and 57 soft tissue characters (the latter from Wetterer *et al.*, 2000). These data support monophyly of the subfamilies Brachyphyllinae, Phyllostominae, and Glossophaginae, and the tribes Glossophagini and Lonchophyllini. Our analysis contradicts the phylogeny estimated from the RAG-2 gene, which does not support a monophyletic Glossophaginae (Baker *et al.*, 2000). Parsimony analysis of a combined matrix, containing morphological characters and RAG-2 sequences, results in a phylogeny that includes Brachyphyllinae and Phyllostominae in Glossophaginae. Support for most clades is stronger than in the morphological tree, but support for basal nodes of the phylogeny remains weak. The weak support at these basal nodes underscores the historical disagreements regarding relationships among these taxa; combining morphological and molecular data has not improved support for these nodes. Uncertainty regarding basal relationships complicates description of morphological change during the evolution of nectarivory in the Phyllostomidae.

KEY WORDS: Phyllostomidae, Glossophaginae, Brachyphyllinae, Phyllostominae, nectar-feeding, RAG-2.

INTRODUCTION

The taxonomic history of the nectar-feeding phyllostomid bats has been dominated by questions pertaining to the relationships among three major groups (Table I), the Caribbean subfamilies Brachyphyllinae and Phyllostominae and the more broadly distributed Glossophaginae. There has been little consensus regarding relationships among these groups. Some researchers have included *Brachyphylla* in the subfamily Phyllostominae (Silva-Taborda and Pine, 1969; Smith, 1976; Corbet and Hill, 1980; Baker *et al.*, 1981), some have elevated *Brachyphylla* to a monotypic subfamily (Simpson, 1945; de la Torre, 1961; Koopman and Jones, 1970; Griffiths, 1982, 1983; Gimenez *et al.*, 1996;

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Wetterer *et al.*, 2000), and others have argued that *Brachyphylla* and Phyllonycterinae form a clade within the Glossophaginae (Gardner, 1977; Baker and Bass, 1979; Honeycutt and Sarich, 1987; McKenna and Bell, 1997; Baker *et al.*, 2000). Further, species of the genera *Lionycteris*, *Lonchophylla*, and *Platalina* have been considered a clade either distinct at the subfamily level (Lonchophyllinae, Griffiths, 1982) or more recently, as a tribe within the Glossophaginae (Lonchophyllini, Wetterer *et al.*, 2000).

Several researchers have used data from morphological or molecular sources to reject the monophyly of Glossophaginae (Baker, 1967; Phillips, 1971; Griffiths, 1982; Baker *et al.*, 2000). The most specialized members of the Glossophaginae have been placed into a single tribe, Glossophagini, by Wetterer *et al.* (2000). Based on molecular studies, however, Baker (pers. commun.) has suggested that this arrangement results in a classification that is paraphyletic at several levels. Among his recommendations is

Table I. Taxonomy of Nectar-Feeding Phyllostomid Bats^a

Subfamily	Tribe	Genus	Species
Brachyphyllinae		<i>Brachyphylla</i>	<i>cavernarum</i> <i>nana</i>
Phyllonycterinae		<i>Phyllonycteris</i>	<i>aphylla</i> <i>poeyi</i>
		<i>Erophylla</i>	<i>bombifrons</i> <i>sezekorni</i>
Glossophaginae	Glossophagini	<i>Anoura</i>	<i>caudifer</i> <i>cultrata</i> <i>geoffroyi</i> <i>latidens</i>
		<i>Choeronycteris</i>	<i>mexicana</i>
		<i>Choeroniscus</i>	<i>godmani</i> <i>minor</i> <i>periosus</i>
		<i>Hlonycteris</i>	<i>underwoodi</i>
		<i>Lichonycteris</i>	<i>obscura</i>
		<i>Musonycteris</i>	<i>harrisoni</i>
		<i>Scleronycteris</i>	<i>ega</i>
		<i>Glossophaga</i>	<i>commissarisi</i> <i>leachii</i> <i>longirostris</i> <i>morenoi</i> <i>soricina</i>
		<i>Leptonycteris</i>	<i>curasoeae</i> <i>nivalis</i> <i>yerbabuena</i>
		<i>Monophyllus</i>	<i>plethodon</i> <i>redmani</i>
	Lonchophyllini	<i>Lionycteris</i>	<i>spurelli</i>
		<i>Lonchophylla</i>	<i>handleyi</i> <i>hesperia</i> <i>mordax</i> <i>robusta</i> <i>thomasi</i>
		<i>Platalina</i>	<i>genovensium</i>

^aAfter Wetterer *et al.* (2000).

the division of Glossophagini into two groups, which we will here refer to informally as “glossophagines” (genera *Glossophaga*, *Leptonycteris*, and *Monophyllus*) and “choeronycterines” (genera *Anoura*, *Choeronycteris*, *Choeroniscus*, *Hylonycteris*, *Lichonycteris*, *Musonycteris*, and *Scleronycteris*).

Questions regarding relationships among nectar-feeding phyllostomid bats continue to intrigue systematists for several reasons. These bats represent the largest radiation of mammalian nectarivores; their wide range of specialization provides a unique opportunity to study the evolution of nectar-feeding behavior. They occupy an array of habitats, from the southwestern United States to the Amazon basin, permitting comparisons among bats feeding in different ecosystems. The group includes several island taxa, thus presenting the opportunity for addressing questions about island biogeography. A well-resolved phylogeny is needed to provide an historical context for these studies.

Three components of this phylogeny are of special interest. First is the placement within Phyllostomidae of the clades Brachyphyllinae, Phyllonycterinae, Lonchophyllini, and the two subgroups within Glossophagini referred to by Baker (pers. commun.) as glossophagines and choeronycterines. Data from different sources offer conflicting hypotheses of relationship among these five groups, while at the same time supporting each of the five as a separate, well-defined clade. Resolution of the relationships among these basal groups is critical for understanding the origin of nectarivory in phyllostomid bats. A second question of special interest concerns placement of the island genera (*Brachyphylla*, *Phyllonycteris*, *Erophylla*, and *Monophyllus*); how are these island taxa interrelated and how many independent colonization events are required to explain their occurrence in the Caribbean? Finally, an understanding of relationships among the most specialized of the nectar-feeding bats (the choeronycterine genera *Anoura*, *Choeronycteris*, *Choeroniscus*, *Hylonycteris*, *Lichonycteris*, *Musonycteris*, and *Scleronycteris*) would provide an historical framework for exploring the evolution of features associated with obligate nectarivory.

The nectar-feeding phyllostomids exhibit a wide range of dietary specialization. One persistent difficulty in studying the evolution of these feeding strategies is the flexibility of diet in most species in the Phyllostomidae. Some species that are primarily frugivorous or insectivorous, such as *Phyllostomus discolor*, occasionally supplement their diet with nectar (Heithaus *et al.*, 1974, 1982; Hopkins, 1984; Ramirez *et al.*, 1984; Buzato and Franco, 1992; Gribel and Hay, 1993; Valiente-Banuet *et al.*, 1997; Gribel *et al.*, 1999). These ‘generalist’ species access nectar by landing on the plant and draining the corolla (Heithaus *et al.*, 1974; Voss *et al.*, 1980; Fisher, 1992; Machado *et al.*, 1998; Gibbs *et al.*, 1999). At the other end of the spectrum are the specialized nectarivores, bats that seem to include a significant amount of nectar in their diet. Specialized nectarivores hover at the flower while feeding and drink small quantities of nectar at each corolla. They are much more effective pollinators than are generalists (Heithaus, *et al.*, 1982; Herrera and Del Rio, 1998) and their pollination services have allowed them to influence the size, shape, density, and nectar concentrations of their host plants (Hopkins, 1984; Eguiarte and Burquez, 1987; Gribel and Hay, 1993; Luckow and Hopkins, 1995). In turn, the morphology of their host plants has probably influenced the evolution of bat structures associated with nectar feeding. The bats examined here represent the entire range of specialization for nectarivory, from species that occasionally consume nectar, e.g., *Brachyphylla cavernarum* (Nellis and Ehle, 1977), to species that rely on nectar as the main component of their diet, e.g., *Hylonycteris underwoodi* (Jones and Homan, 1974).

Morphological specializations of the nectarivorous phyllostomid bats are extraordi-

nary. These include an elongated and extensile tongue, often with brush-like papillae on the tip, an elongated rostrum, reduction or loss of the incisors, reduction of the molars and premolars, and the ability to hover efficiently while feeding (Griffiths, 1982; Gimenez *et al.*, 1996; Phillips, 1971; Winter, 1998; Winter *et al.*, 1998). The potential for convergence in morphological features associated with nectarivory seems high. If convergence is common for these features, then phylogenies based on them are likely to mislead with respect to historical relationships among species (e.g., Brooks and McLennan, 1991).

In this study, we generate a phylogeny of nectar-feeding phyllostomid bats based on 119 morphological characters (62 collected here and 57 taken from Wetterer *et al.*, 2000). We investigate this phylogeny for evidence that it has been biased by convergence in morphological features associated with nectar feeding and compare it to a phylogeny based on nuclear DNA sequence data from Baker *et al.* (2000). The morphological and molecular data are subsequently combined and the resulting phylogeny used to examine features of dental evolution in nectar-feeding bats.

MATERIALS AND METHODS

We collected character data from the skulls of representatives of 35 species of phyllostomid nectar-feeding bats (Table I), with monophyly of the Phyllostomidae assumed (Simmons, 1998; Simmons and Geisler, 1998). One mormoopid (*Pteronotus parnellii*) and six phyllostomids (*Artibeus hirsutus*, *Carollia brevicauda*, *Desmodus rotundus*, *Lonchorhina aurita*, *Macrotus californicus*, and *Phyllostomus discolor*) were used as outgroup species. Outgroups were chosen based on their hypothesized relationships to the nectar-feeding phyllostomid bats, and included at least one member from each phyllostomid subfamily (Wetterer *et al.*, 2000). *Lonchorhina aurita* was chosen to investigate the sister relationship between that species and Lonchophyllini found in the phylogeny estimated from the RAG-2 gene. All phylogenies presented here were rooted with *Pteronotus spp.*

Due to the high degree of character variability within certain genera, species were used as terminal taxa in the analysis of the morphological data. Where possible all recognized species were sampled from each genus (Koopman, 1993; Novak, 1994); however, two species of *Phyllonycteris* (*P. major* and *P. obtusa*) and three species of *Lonchophylla* (*L. dekeyseri*, *L. concava*, and *L. bokermanni*) were not available to us.

Sixty-two characters from the skin, skull, and dentition of the nectar-feeding phyllostomid bats were coded (see Appendix I for descriptions). Characters 13, 22, 24, 25, 26, 28, 31, 41, 42, 45, 46, 50, 58, and 61 were based on descriptions found in Phillips (1971). Characters were required to be identifiable across the ingroup. Most characters were binary with presence / absence coding, but in several cases, an additional character state was used to designate an alternative form of a character. All characters were unordered and equally weighted. Characters that were polymorphic within a species were scored with an additional character state in the data matrix. All specimens were examined at least two times; characters that were scored inconsistently were eliminated from the study. Taxa that were missing an anatomical feature on which another character was based were coded as missing in the data matrix (e.g., taxa without lower incisors were coded as missing for all characters that concern the crowns of the lower incisors). We adopted this procedure to avoid artificial weighting of these missing characters. Charac-

ters that we hypothesized to be correlated (for example the presence of the same character on each of three molars) were coded only one time. In general, characters were coded in a reductive manner following Wilkinson (1995).

In addition to these 62 characters of the skin, skull, and dentition, 57 soft-tissue characters were taken directly from Wetterer *et al.* (2000). The complete data matrix (119 characters \times 42 taxa) was missing 139 data points (2.8%). Character states were recorded using MacClade version 3.04b (Madison and Madison, 1992).

The morphological data were subjected to a parsimony analysis using the heuristic search option in PAUP*4.0b, with 100 random addition replicates and TBR branch swapping (Swofford, 2002). PAUP* was used to calculate tree statistics, including tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC), and the strict consensus of the most parsimonious trees. Clade stability was assessed using bootstrap analysis (Felsenstein, 1985) and Bremer decay analysis (Bremer, 1988). PAUP* was used to perform 7862 replicates of the bootstrap analysis. Bremer decay indices were computed with TreeRot v.2 (Sorenson, 1999).

It has been suggested that the nectar-feeding phyllostomid bats have converged to a similar morphology because they share a feeding niche (Baker, 1967; Winkelman, 1971; Griffiths, 1982; Baker *et al.*, 2000). To investigate the effects of convergence on our phylogeny, the morphological data were partitioned into two groups: 36 characters likely to be directly associated with nectarivory (Table II), and the remaining 83 characters, which have no obvious association with nectar feeding. A partition homogeneity test was performed with PAUP* to assess character congruence between these two data sets. The test included 1000 replicates; searches were heuristic with simple taxon addition and TBR branch swapping. The data, excluding the 36 characters likely to be associated with nectar feeding, were then searched for the most parsimonious tree.

DNA sequence data (1363 base pairs from the RAG-2 gene) were downloaded from GenBank (AF316433–AF316479; Baker *et al.*, 2000) and two statistical techniques were used to compare the topologies of phylogenies estimated from the morphological and RAG-2 data. First, a partition homogeneity test was performed (as above) on the morphological and molecular partitions of the combined data to evaluate character congruence between data sets. Second, a parametric bootstrap analysis was performed on the molecular data to test the null hypothesis that the topology identified by the

Table II. Morphological Characters that are Susceptible to Convergence in Bats that Specialize on Nectar^a

#20	Medial gap between lower incisors
#21	Number of lower incisors
#23	Position of the crowns of the lower incisors
#41	Medial gap between upper incisors
#42	Shape of upper inner incisors
#44	Height of the crowns of the upper incisors
#66–81	Characters of the musculature in the hyoid region
#82–95	Characters of the tongue

^aNumbers refer to Appendix I.

morphological data was not significantly different from the topology identified by the molecular data (Huelsenbeck *et al.*, 1996; Sullivan *et al.*, 2000). In order to identify the appropriate model of sequence evolution to use in the simulations, we estimated the molecular phylogeny with a neighbor-joining tree and computed the log-likelihood score for each of 16 models of sequence evolution (Sullivan *et al.*, 1997). Using a χ^2 approximation of the null distribution (Yang *et al.*, 1995), we used a likelihood ratio test of goodness of fit to identify the simplest model of sequence evolution that was not significantly worse than the GTR + I + Γ model. As all models with fewer parameters were significantly worse than the GTR + I + Γ model, Seq-Gen (Rambaut and Grassly, 1997) was used to generate 1000 simulated data sets under this model. The following model parameters were identified by PAUP* and used in the creation of the simulated data sets: equilibrium base frequencies (A = 0.290068, C = 0.240716, G = 0.22514, T = 0.244076), rate ratio parameters ($r(AC) = 1.39393$, $r(AG) = 7.02043$, $r(AT) = 0.547676$, $r(CG) = 1$, $r(CT) = 7.02043$, $r(GT) = 1$), invariable sites (= 0.362042), and rates across variable sites ($\alpha = 0.723386$). Each simulated data set was searched for two trees: the most parsimonious tree (TL_{MP}) and the most parsimonious tree with a topology constrained to match the topology predicted by the morphological data (TL_C). The difference between these two tree lengths ($TL_C - TL_{MP}$) was used to generate a null distribution. The percentage of trees with a $TL_C - TL_{MP}$ greater than or equal to the $TL_C - TL_{MP}$ in the actual data served as the test statistic, and this was evaluated at the 5% significance level.

RAG-2 sequences were available for 18 of the 45 species present in the morphological data set, and we combined these sequences with the corresponding morphological data. Specimens from two species sequenced by Baker *et al.*, (2000) were not available for examination, so we combined morphological data from *Pteronotus parnellii* and *Phyllostomus discolor* with RAG-2 sequences from *Pteronotus dayvi* and *Phyllostomus hastatus*. The resulting molecular data matrix (20 taxa, 262 informative characters) was searched for the most parsimonious tree using the same techniques as indicated above for the morphological data. Finally, the 36 characters associated with nectar feeding (Table II) were partitioned from the remaining 226 parsimony-informative characters to examine their effects on the combined-data topology.

In addition to this restricted combined data matrix, we analyzed a “super matrix” that contained all available morphological data and the corresponding RAG-2 data (46 taxa), using the same methods as the other searches. While this “super matrix” is more inclusive with respect to taxa, it has a significant amount of missing data (> 50%).

RESULTS

A heuristic search of the morphological data identified 384 most parsimonious trees with a length of 354, a CI of 0.446, a RI of 0.801, and a RC of 0.357. A strict consensus is shown in Figure 1. This tree supports the monophyly of Brachyphyllinae, Phylloncyterinae, Lonchophyllini, the choeronycterines, and the glossophagines. In this manner it is consistent with the molecular phylogeny (based on RAG-2; Baker *et al.*, 2000; Figure 2) in supporting these five clades; however, the two phylogenies differ markedly in the placement of these clades relative to one another. In the morphology-based phylogeny, both Glossophagini and Glossophaginae are monophyletic, and the placement of Brachyphyllinae and Phylloncyterinae can not be resolved. In the molecular phylogeny, Brachy-

phyllinae and Phyllonycterinae form a clade with the glossophagines, and *Lonchophyllini* is more closely related to *Lonchorhina aurita* than to any of the nectar-feeding phyllostomids.

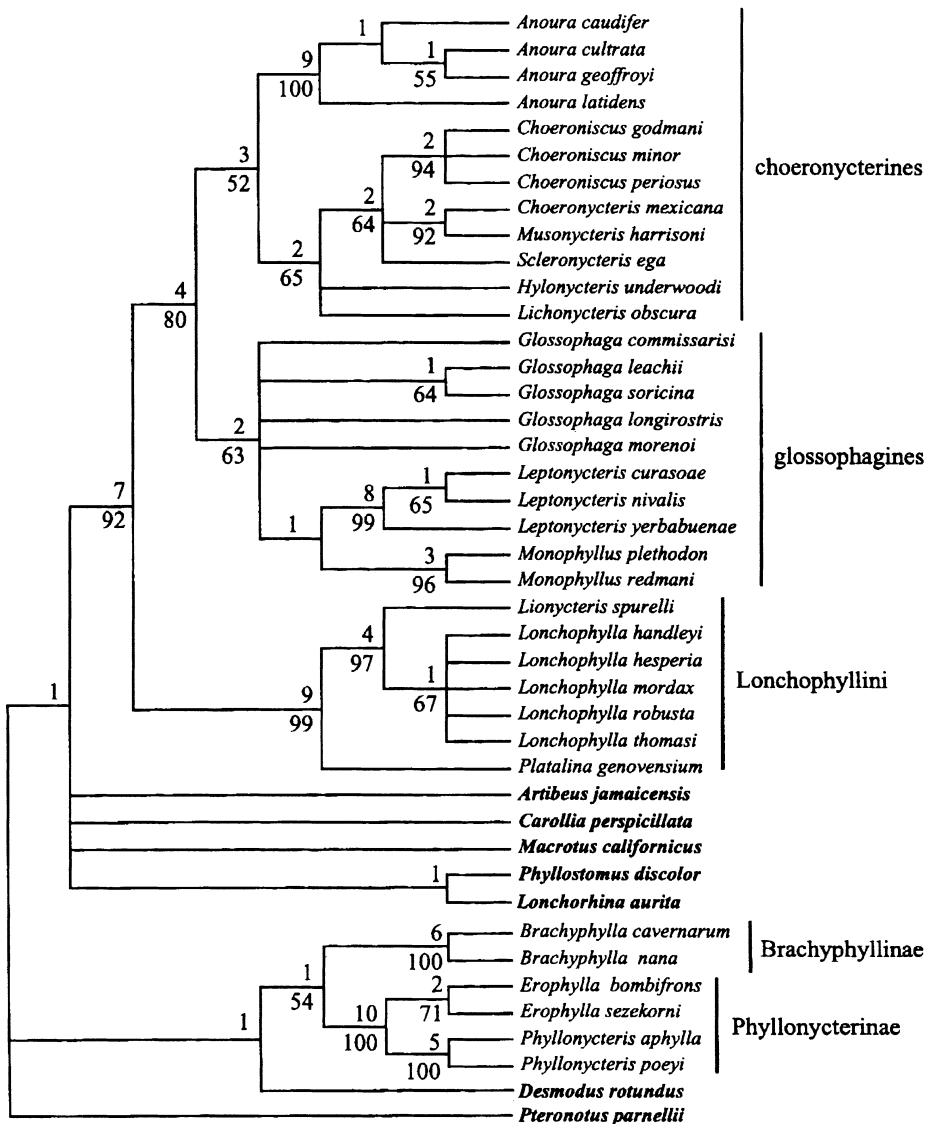


Fig. 1. Strict consensus of the 384 most parsimonious trees from an analysis of 119 skull and soft tissue characters. Tree length = 354; Consistency index = 0.446; Retention index = 0.801; Rescaled consistency index = 0.357. Bremer decay indices are given above each non-terminal clade. Bootstrap proportions from 7862 replicates are given below clades found in greater than 50% of the replicates. Outgroup taxa are shown in bold type.

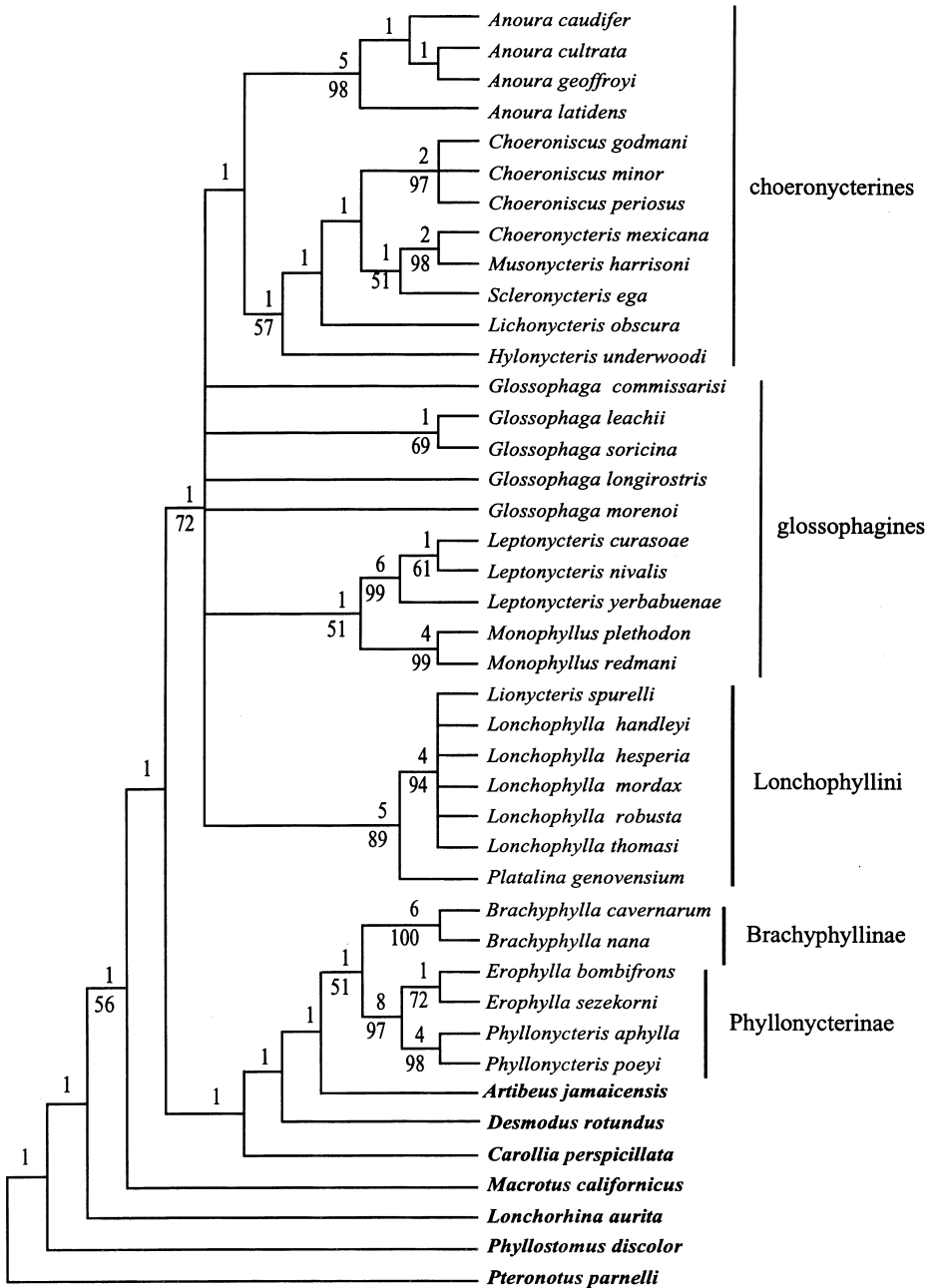


Fig. 3. A strict consensus of the 267 most parsimonious trees from a search of the morphological characters, excluding those thought to be associated with nectar feeding (Table II). Tree length = 265; Consistency index = 0.415; Retention index = 0.744; Rescaled consistency index = 0.309. Bremer decay indices are given above each non-terminal clade. Bootstrap proportions from 1000 replicates are given below clades found in greater than 50% of the replicates. Outgroup taxa are shown in bold type.

Despite these findings, we continued with the combined analysis after observing that many of the same clades were identified by both phylogenies, and where conflicts occurred, the conflicting nodes were poorly supported by one or both data sets.

A branch and bound search of the combined morphological and molecular data identified a single most parsimonious tree with a length of 651, a CI of 0.495, a RI of 0.617, and an RC of 0.305 (Figure 4). For most clades, support indices are higher, often much higher, than those found in the tree based on morphological data alone. The major difference between this phylogeny and the phylogeny based on morphology alone is the inclusion of the genera *Brachyphylla* + *Erophylla* + *Phyllonycteris* in the subfamily Glossophaginae as the sister clade to the tribe Glossophagini (sensu Wetterer *et al.*, 2000). Support for all basal nodes is weak in the combined phylogeny (Bremer = 1 and bootstrap < 50%).

Because characters associated with nectar feeding (Table II) defined some of the basal relationships in the phylogeny based on morphological data alone, we searched the combined morphological and molecular data after excluding those characters. The resulting tree (Fig. 5) is similar to the combined-data phylogeny (Figure 4) in that every clade that is moderately or well-supported in the combined tree (i.e., Bremer > 2, bootstrap > 70) is retained except for the sister group relationship between the choeronycterine bats and the glossophagine bats, which collapses when the 36 characters associated with nectar feeding are excluded.

The phylogeny estimated from the “super matrix” (not shown) is almost identical to the phylogeny based on morphology alone (Figure 1). This is not surprising, since two-thirds of the informative characters are from the morphological data set. The only clade from the phylogeny estimated from the “super matrix” that is not present in the phylogeny estimated from the morphological data is a clade uniting several of the outgroup genera to Brachyphyllinae + Phyllonycterinae. As in the other estimates of phylogeny, support values for basal nodes in this phylogeny are low.

DISCUSSION

While there is considerable concordance between the molecular and morphological phylogenies, these data sets offer conflicting hypotheses of relationship among the major clades of phyllostomid nectar-feeding bats. The phylogeny estimated from the RAG-2 data (Figure 2) suggests that Brachyphyllinae and Phyllonycterinae share a close relationship to Glossophagini and that Lonchophyllini is sister to *Lonchorhina*. The morphological data (Figure 1) support a monophyletic Glossophaginae, thus excluding Brachyphyllinae, Phyllonycterinae, and *Lonchorhina* from the Glossophaginae. A monophyletic Glossophaginae is recovered even when characters thought to be associated with nectar feeding are removed from the morphological analysis (Figure 3).

Two methods (the partition homogeneity test and the parametric bootstrap) were used to examine differences between the RAG-2 and morphological data sets. These methods suggest that there are significant differences in both the congruence of characters and the estimate of phylogeny from the morphological and molecular data. In spite of these differences, we feel that there are important reasons to combine the available data. The partition homogeneity test has been criticized as an inappropriate way to assess the potential to combine data from different sources (Sullivan, 1996), in large part because separate

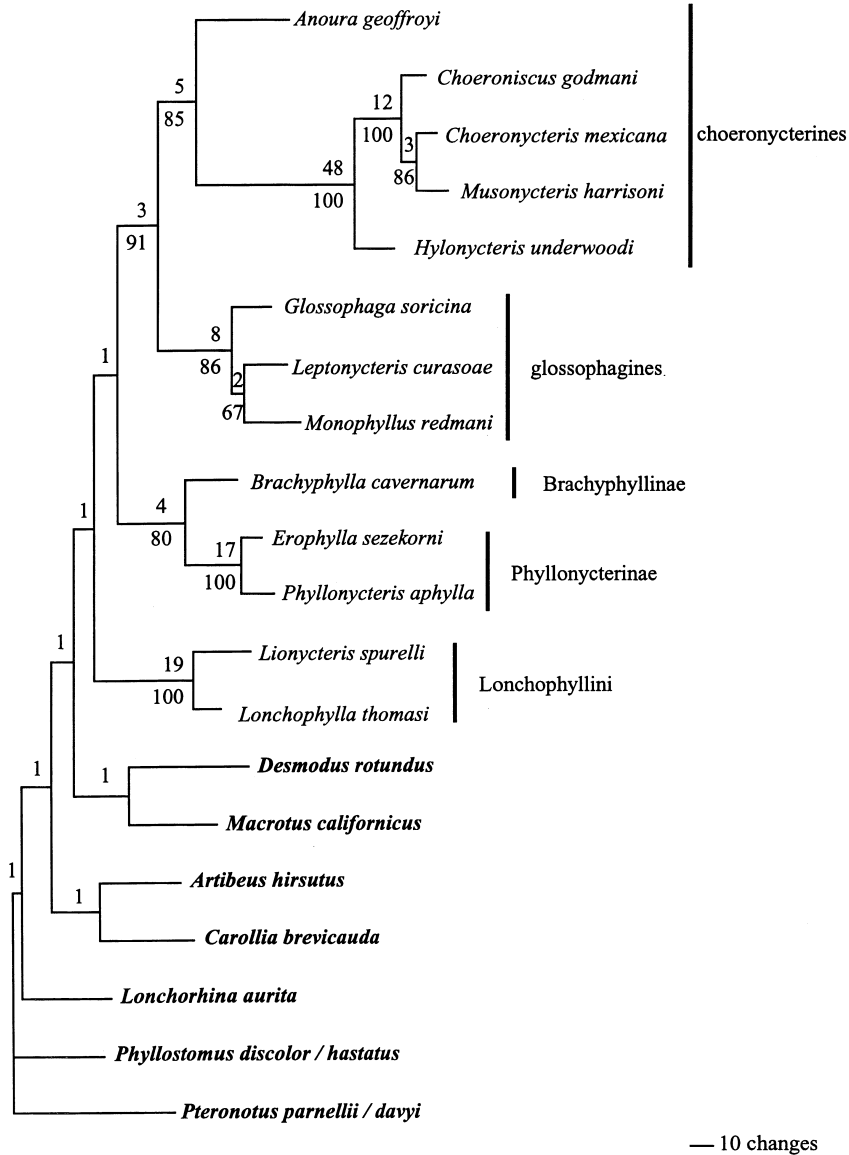


Fig. 4. The most parsimonious trees from a branch and bound search of 262 informative characters: 143 from the RAG-2 gene and 119 morphological. Tree length = 651; Consistency index = 0.495; Retention index = 0.617; Rescaled consistency index = 0.305. Bremer decay indices are given above each non-terminal clade. Bootstrap proportions from 10000 replicates are given below clades found in greater than 50% of the replicates. Outgroup taxa are shown in bold type.

data sets can be incongruent but still improve the overall estimation of phylogeny when combined. While the parametric bootstrap shows that the topology estimated from the RAG-2 data is significantly different from the topology estimated from the morphologi-

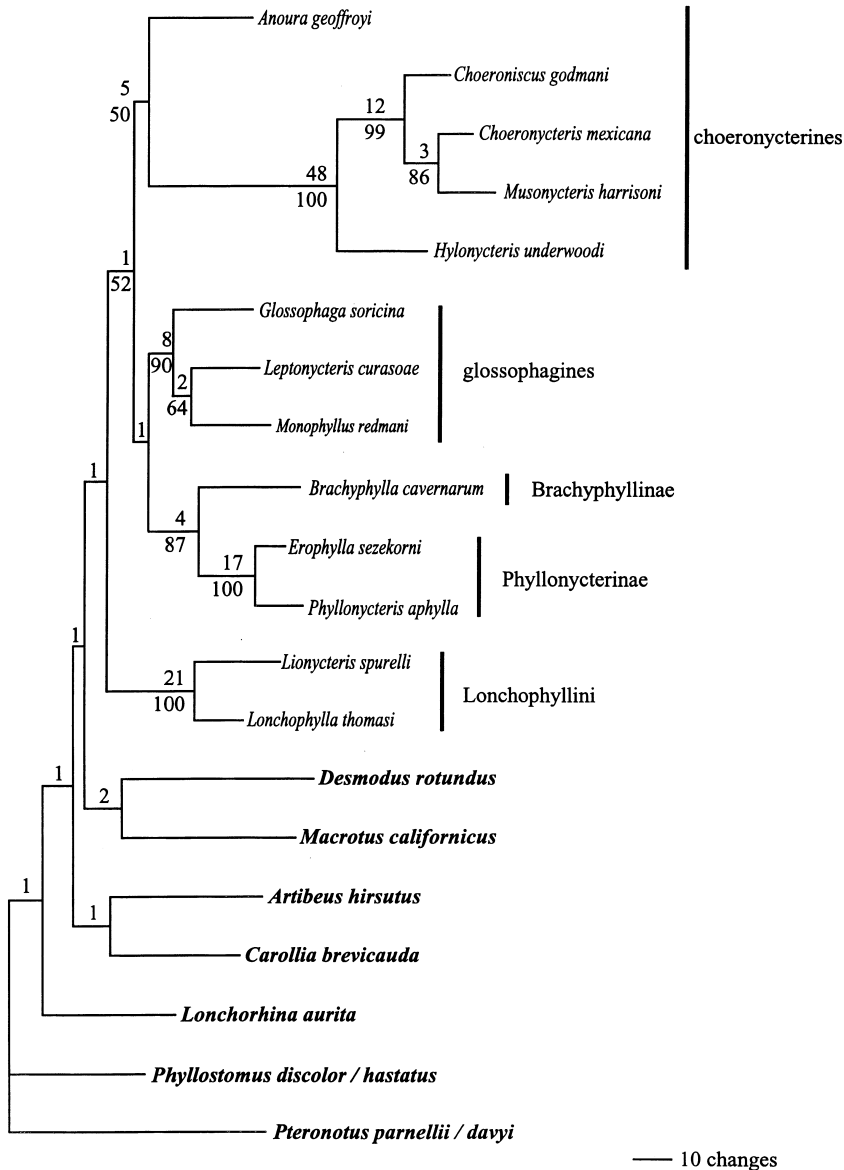


Fig. 5. The most parsimonious trees from a search of the combined data (RAG-2 + morphology), excluding those characters thought to be associated with nectar feeding (Table II). Tree length = 741; Consistency index = 0.603; Retention index = 0.585; Rescaled consistency index = 0.353. Bremer decay indices are given above each non-terminal clade. Bootstrap proportions from 1000 replicates are given below clades found in greater than 50% of the replicates. Outgroup taxa are shown in bold type.

cal data, it may also be inappropriate as a way of assessing the potential to combine data sets. One immediate concern is that it is not possible to perform the opposite test (to test the null hypothesis that the phylogeny estimated by the morphological data is

significantly different than the phylogeny estimated by the RAG-2 data) because we can not simulate morphological data. A more philosophical concern is related to the nature of phylogeny estimation. Following Felsenstein (1982), we consider phylogenies to be an estimate of the true parameter in the multi-dimensional treespace that surrounds the actual evolutionary relationships of the species in question. Data from different sources provide different point estimates in this cloud of treespace; it is analogous to parameter estimates from different samples of the same population. When viewed in this way, combining data is a way to summarize point estimates from different data sets. Our decision to combine the molecular and morphological data was supported by the observation that many of the same clades were identified by both phylogenies, and where conflicts occurred, the conflicting nodes were poorly supported by one or both data sets.

The phylogeny estimated from the combined data (Fig. 4) suggests that the four genera of nectarivorous phyllostomids endemic to islands in the Caribbean do not form a monophyletic group. Rather, these island taxa are distributed in two separate clades [(*Brachyphylla*, *Phyllonycteris*, *Erophylla*) and (*Monophyllus*)], suggesting two independent colonization events. Both morphological and molecular data place *Monophyllus* with the other glossophagine bats, but placement of the clade that includes *Brachyphylla*, *Phyllonycteris*, and *Erophylla* is problematic. Morphological and molecular data do not agree, and neither data set provides a well-supported hypothesis. This key issue needs resolution before a complete understanding of the evolution of the nectar-feeding phyllostomid bats can be reached.

Until nuclear sequence data were acquired (Baker *et al.*, 2000), the most specialized of the nectar-feeding phyllostomid bats were placed into a single tribe, Glossophagini (Wetterer *et al.*, 2000). Baker (pers. commun.) divided these bats into two groups based on the presence or absence of lower incisors, a glossophagine group for those species that retain lower incisors and choeronycterine group for those without lower incisors. Our analysis supports this division of the Glossophagini into two clades, one composed of the genera *Anoura*, *Choeroniscus*, *Choeronycteris*, *Hylonycteris*, *Lichonycteris*, *Musonycteris*, and *Scleronycteris*, and a second containing the genera *Glossophaga*, *Leptonycteris*, and *Monophyllus*. These clades are recovered by both the morphological and molecular data analyses (Fig. 1 and 2) and there is strong support for both in the combined analysis (Fig. 4; Bremer = 5, bootstrap = 85 for the choeronycterines; Bremer = 8, bootstrap = 86 for the glossophagines).

The placement of these two clades with respect to the other major clades of nectar-feeding phyllostomids is less certain, as morphological and molecular data do not agree. In the combined-data analyses (Fig. 4), they are sister taxa, thus supporting monophyly of the more inclusive Glossophagini (sensu Wetterer *et al.*, 2000), but this relationship collapses when the 36 morphological characters thought to be associated with nectar feeding are removed from the combined-data analysis (Fig. 5). We use the combined-data phylogeny as an historical framework for examining incisor evolution in nectar-feeding phyllostomid bats, recognizing that the nodes connecting these two clades are especially tentative.

The combined-data phylogeny (Fig. 4) suggests an overall trend toward reduction in the incisors that culminates in the choeronycterines. Most phyllostomids, including many nectar-feeding bats, have incisors that are well developed (e.g., *Brachyphylla cavernarum*). In the choeronycterines and glossophagines the upper incisors are reduced in size, and in some cases appear to have migrated laterally, leaving a distinctive gap

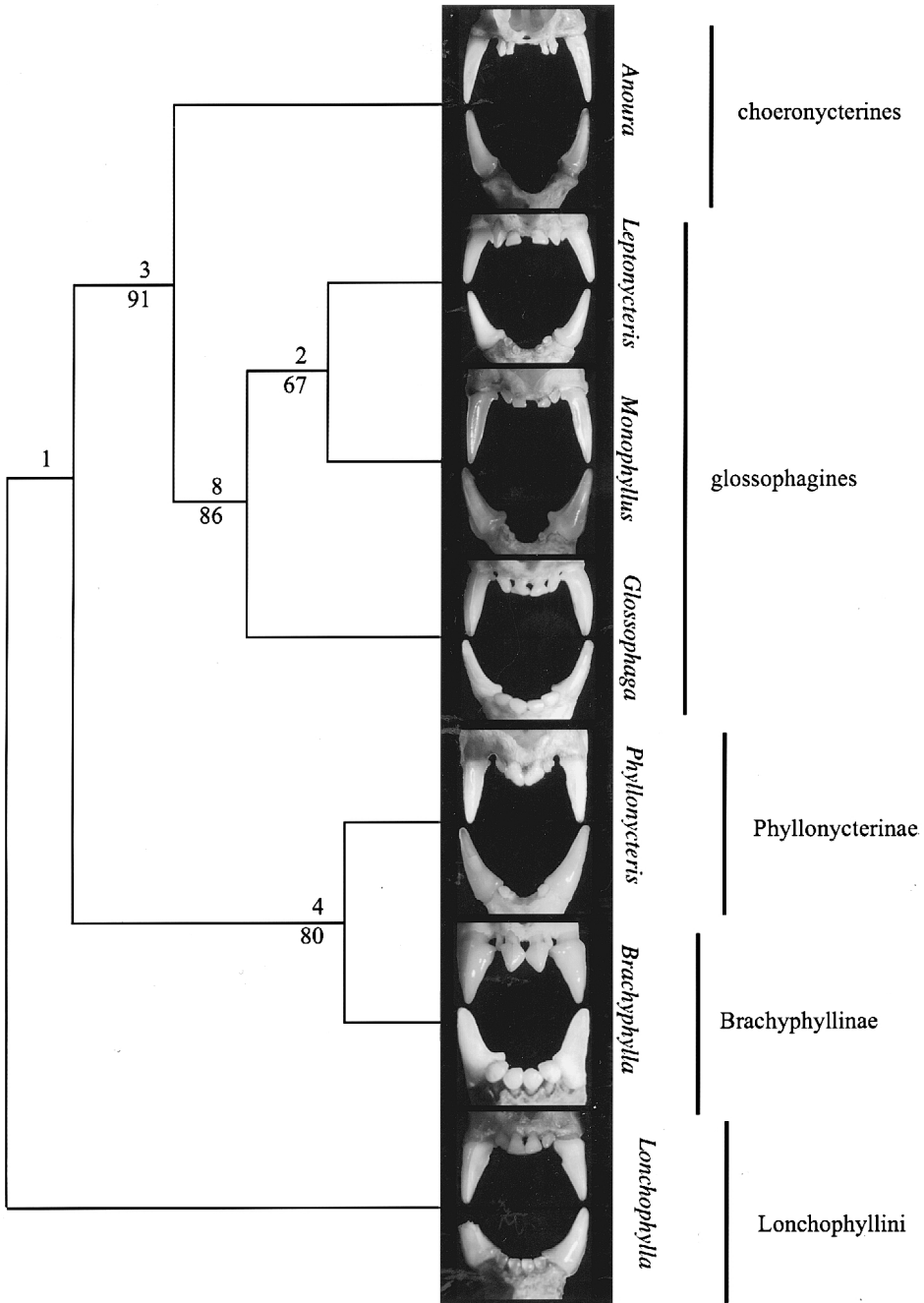


Fig. 6. Reduction of incisors shown on the phylogeny from Figure 4. The reduction of the incisors in the choeronycterines has resulted in an increase in the size of the frontal gap.

between the front teeth. The lower incisors are reduced in the genera *Glossophaga*, *Monophyllus*, and *Leptonycteris*, and in the choeronycterine genera they are missing entirely. The net effect of these changes is to increase the amount of space between the canine teeth (Figure 6). This increase in space is thought to be an adaptation for increased efficiency during feeding, facilitating free movement of the tongue (Freeman, 1995).

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APPENDIX I: CHARACTER DESCRIPTIONS

1. Uropatagium—(0) unreduced, (1) reduced, (2) greatly reduced. The uropatagium of most nectar-feeding phyllostomid bats is reduced in size compared to that of many other members of the family. Bats such as *Anoura geoffroyi* lack a calcar, and the uropatagium of these species is reduced and closely follows the hind legs (2). The uropatagium of most glossophagines, such as *Lonchophylla thomasi*, is complete to or below the level of the knees, giving it the appearance of having an inverted “u” shape (1). These bats usually have a well-developed calcar (see character number 2), which is perpendicular to the tibia and supports the distal end of the patagium in a manner similar to other phyllostomid bats. Unreduced uropatagia extend to the feet or beyond, as in *Macrotus californicus* (0).

2. Calcar—(0) equal to or longer than foot, (1) shorter than foot, or (2) absent (Straney, 1980; Wetterer *et al.*, 2000). The calcar, a spur of cartilage or bone that projects from the ankle and supports the uropatagium, is equal to or longer than the length of the foot in most phyllostomid bats (0). In most nectar-feeding bats a calcar is present, but it is shorter than the length of the foot (1). Exceptions include *Phyllonycteris spp.* and *Brachyphylla spp.*, in which the only evidence of a calcar is a small bony protrusion on the ankle (2), possibly homologous with a true calcar.

3. Tail—(0) enclosed in uropatagium, (1) extends beyond uropatagium, or (2) absent (Straney, 1980; Wetterer *et al.*, 2000). The tail of most glossophagines is short and enclosed in the uropatagium (0). In *Macrotus*, the tail extends beyond the uropatagium (1). In other nectar-feeding phyllostomid bats (most *Anoura* and *Leptonycteris*), no tail is visible (2).

4. Premaxillary region with third foramina—(0) absent, or (1) present. Three foramina are present in the premaxillary region of the cranium in most members of the Glossophaginae (1). These foramina are oriented in a triangle, with the most anterior foramen just posterior to the upper incisors. *Lichonycteris obscura*, *Lionycteris spurelli*, and *Scleronycteris ega* all lack the most anterior foramen, as do Brachyphyllinae and Phyllostomycterinae (0). This appears to be the ancestral condition for Phyllostomidae, as all members of the outgroup have two foramina in their premaxilla.

5. Foramen between the foramen ovale and mandibular fossa—(0) absent, or (1) present. Several foramina are found at the base of the skull of phyllostomid bats. All nectar-feeding bats have a large foramen, the foramen ovale, on either side of the palatine. A smaller foramen is sometimes found posterior to it, between the anterior portion of the pterygoid and the mandibular fossa (1). This may be formed by a projection of bone across the foramen ovale. Several taxa lack this foramen (0).

6. Foramen at the anterior margin of the orbital region—(0) absent, or (1) present. While nectar-feeding phyllostomid bats lack an orbital process, two taxa (*Choeronycteris mexicana* and *Musonycteris harrisoni*) have a foramen in the approximate place where the orbital process occurs in other bats (1). Other taxa lack this foramen (0).

7. Foramen between the inner incisors—(0) absent, or (1) present. In most bats with three foramina in their premaxillary region (character 4), the most anterior foramen is located posterior to the first upper incisors (0). In some species of the genera *Anoura* and *Choeroniscus*, the most anterior foramen is located between the inner incisors (1). This character is sometimes polymorphic within species, as some specimens of *Anoura* spp. and *Choeroniscus* spp. that lack this foramen have a 'v'-shaped indentation in the premaxilla. This is interpreted to be an incomplete formation of the premaxilla as a result of this most anterior foramen and is coded (1).

8. Anterior projection of lower portion of the mandible—(0) absent, or (1) present. The mandible of some choeronycterines, such as *Lichonycteris obscura*, has a bony protrusion extending anteriorly and ventrally in lateral view, so that the anterior limit of the dentary is near its ventral margin and extends well beyond the incisors (1). Most species lack a projection and the most anterior point of the dentary is medial (0).

9. Lateral compression of region separating the anterior portion of the pterygoids from the rostrum—(0) absent, or (1) present. The dorsal region between the anterior portion of the pterygoids and the posterior portion of the palatine is laterally compressed in members of the genus *Phyllostomycteris*, which results in a slight separation of this region from the sphenoid region (1). In lateral view, this appears to be a foramen. Other phyllostomid bats lack this separation (0).

10. Presphenoid ridge—(0) absent, or (1) present. Many nectar feeders have a longitudinal ridge along the midline of the presphenoid region that is elevated above the base of the presphenoid (1). The presphenoid ridge is lacking in some genera, including *Anoura* and *Choeroniscus* (0). Much like the basioccipital region in character 16, the presphenoid region often has a slightly thickened medial portion. This differs from the well-developed ridge of taxa like *Glossophaga soricina* in that it does not extend above the surrounding presphenoid region.

11. Pterygoid alae—(0) absent, or (1) present (Alvarez *et al.*, 1991). The posterior part of the pterygoid of *Glossophaga soricina* and *Glossophaga leachii* has small projec-

tions (alae) that protrude towards the auditory bullae (1). Other phyllostomid bats lack these protrusions on their pterygoids (0).

12. Peninsular fusion of the posterior edge of the palatine bone—(0) absent, or (1) present. The palatine region of most nectar feeding bats is fused in such a manner that the anterior-most point along the posterior margin of the palatine is contained within an arc running from the lingual portion of the fusion of the palatine with the pterygoid (0). In the genus *Anoura*, the posterior margin of the palatine is interrupted by a small peninsula of bone that forms along the medial axis of the palatine region and projects posteriorly between the pterygoids (1).

13. Inflated pterygoid—(0) absent, or (1) present (Wetterer *et al.*, 2000). In *Choeroniscus spp.*, *Choeronycteris mexicana*, and *Musonycteris harrisoni*, the pterygoid is inflated and curves outward, bringing the tip nearly into contact with the anterior margin of the auditory bullae (1). The pterygoids of other nectar feeders are not inflated (0).

14. Protrusion at medial posterior margin of sphenoid region—(0) absent, or (1) present. A bony process at the base of the sphenoid region projects posteriorly over the anterior portion of the occipital bone in several taxa, including *Glossophaga soricina* (1). Most species lack this process (0).

15. Overhanging posterior margin of the sphenoid—(0) absent, or (1) present. The posterior portion of the sphenoid region extends over the anterior portion of the basioccipital in *Choeronycteris mexicana* and *Musonycteris harrisoni*, creating two small pockets on either side of the medial ridge dividing the basioccipital (1). The posterior margin of the sphenoid in other phyllostomid bats, while it may be elevated above the basioccipital, does not extend past the anterior portion of the basioccipital (0).

16. Ridge dividing the basioccipital—(0) absent, or (1) present. A prominent ridge that is narrow and significantly elevated above the level of the basioccipital divides the basioccipital along its medial axis in many taxa, including *Lonchophylla thomasi* (1). This is distinguished from the slightly thickened medial portion of the basioccipital in most phyllostomids by both its elevation and width. Taxa without a prominent ridge are coded (0).

17. Zygomatic arch—(0) absent, or (1) present (Lim, 1993). Most phyllostomid bats have a complete zygomatic arch (1). The arch is incomplete in some nectar feeders, including *Choeroniscus spp.* and *Lonchophylla spp.* (0). When present, it is reduced in robustness. All taxa with a complete zygomatic are coded (1), regardless of the thickness of the arch.

18. Sagittal crest—(0) absent, or (1) present. The sagittal crest is absent in all members of the Glossophaginae and Phyllostominae (0). A sagittal crest is present in most other phyllostomid bats, including the Brachyphyllinae (1).

19. Position of basioccipital and presphenoid—(1) on same horizontal plane, or (0) presphenoid ventral to basioccipital. In the Lonchophyllini, the basioccipital is on the same horizontal plane as the presphenoid (1). In other glossophagines and in the outgroup, the presphenoid is ventral to the basioccipital when seen in lateral view (0).

20. Medial gap between lower incisors—(0) absent, or (1) present. Some taxa that have retained the lower incisors have a median gap between the inner incisors (1). Other taxa with lower incisors lack this gap (0).

21. Number of lower incisors—(0) none, or (2) two (Wetterer *et al.*, 2000). The reduction in number of lower incisors is one of the most noticeable characteristics of the

glossophagine jaw. Freeman (1995) considered this to be the result of selection for the unhindered movement of the tongue during feeding. Most phyllostomid bats have two lower incisors on each side of the mandible (2), but many species of glossophagines are missing the lower incisors entirely (0).

22. Crown on lower incisors—(0) bifid, or (1) trifold. The Lonchophyllini possess a trifold crown on each of their lower incisors (1). On these teeth, two grooves divide the crown of the tooth into three lobes. Other phyllostomid bats lack the trifold crown (0).

23. Position of the crowns of the lower incisors—(0) coplanar, or (1) depressed. The crowns of the inner incisors of some genera, such as *Erophylla spp.*, are lower in elevation than the crowns of the outer incisors, a pattern that results in a shallow ‘u’-shaped incisor row in frontal view (1). In these teeth, the root to tip distance appears equal, but the teeth sit at a lower position in the dentary. Other genera, such as *Lonchophylla*, have incisors with crowns that are coplanar (0).

24. Canines—(0) straight, or (1) curved. The canines of most glossophagine bats appear to be bowed outward, causing them to appear curved in frontal view (1). *Lichonycteris obscura* and *Scleronycteris ega* are exceptions with straight lower canines (0). Most other phyllostomid bats, including the Brachyphyllinae and Phyllostomycterinae, also have straight lower canines.

25. Anterior lingual cingular shelf on lower canines—(0) absent, or (1) present. The lower canines have an anterior lingual cingular shelf that articulates with the shearing surface of the outer upper incisors in *Glossophaga spp.*, *Leptonycteris spp.*, and Lonchophyllini (1). This cingular shelf is absent in other nectar-feeding phyllostomid bats (0).

26. Posterior lingual cingular shelf on lower canines—(0) absent, or (1) present. The lower canines of most phyllostomid nectar feeders have a posterior lingual shelf that occludes with the anterior cingular shelf of the upper canine (1). Species that lack this shelf include members of the genera *Anoura* and *Choeroniscus* (0).

27. Number of lower premolars—(2) two, or (3) three. All members of the Glossophaginae have three lower premolars (3). Other nectar feeders have two (2).

28. Elongated labial cusp on the second lower premolar—(0) absent, or (1) present. *Lionycteris spurelli* and *Brachyphylla spp.* have a large labial cusp on the second lower premolar that extends over half of the height of the lower canine (1). Other nectar-feeding phyllostomid bats lack this cusp (0).

29. Cusps on the lower premolars—(1) approximately equal in height, or (0) middle cusp highest. The three cusps on each lower premolar are at approximately the same elevation in *Choeroniscus spp.* (1). Other glossophagines have premolars in which the middle cusp is significantly higher than the other two (0).

30. Width of lower premolars—(0) equal to molars, or (1) less than molars. The width of the lower premolars is approximately equal to the width of the lower molars in most glossophagines (0). In species with an elongated rostrum, the lower premolars are narrower than the lower molars (1).

31. Lingual margin of first premolar—(0) not concave, or (1) concave. A concave lingual margin on the first premolar in *Leptonycteris spp.* appears to be formed by a labial migration of the medial portion of the tooth (1). Other taxa have no lingual curve to the first premolar (0).

32. Number of lower molars—(2) two, or (3) three. *Leptonycteris spp.* and *Licho-*

nycteris obscura have two lower molars (2), while other nectar-feeding phyllostomid bats have three (3).

33. Parallel raised cristid on first lower molar—(0) absent, or (1) present. The talonid of the first lower molar of *Lonchophylla spp.* and *Lionycteris spurelli* has a raised cristid that occludes with the protocone on the first upper molar (1). Other phyllostomid bats lack this ridge (0).

34. Metaconid on first lower molar—(0) absent, or (1) present. The Phyllonycterinae lack a metaconid on the first lower molar (0). The metaconid is present on the first lower molar of members of the Glossophaginae and Brachyphyllinae (1).

35. Lingual margin of trigonid on the first lower molar—(0) ovoid, or (1) concave. The lingual margin of the trigonid on the first lower molar is concave in species such as *Glossophaga soricina*, which gives the anterior half of the first lower molar the shape of a quarter moon (1). The trigonid is ovoid and the interior margin is not concave in other taxa (0).

36. Gap between first and second lower molars—(0) absent, or (1) present. The first and second lower molars have a significant gap between them in many nectar-feeding bats, such as *Choeroniscus periosus* (1). Other nectar-feeding bats lack this gap; their first and second lower molars are more or less in contact (0).

37. Anterior cingular shelf on trigonid—(0) absent, or (1) present. The second lower molar has an anterior cingular shelf on the trigonid in *Lonchophylla spp.* and *Lionycteris spurelli* (1). Other nectar-feeding phyllostomid bats lack this anterior cingular shelf (0).

38. Height of molar protocone and metacone—(0) approximately equal to other cusps, or (1) elevated far above other cusps. The protocone and metacone are much higher than the rest of the molar in *Choeronycteris mexicana* and *Musonycteris harrisoni* (1). The metacone and protocone are only slightly higher in elevation than the other molar cusps in other phyllostomid bats (0). This character may be obscured in specimens with extremely worn molars.

39. Upper incisor crowns—(0) not pointed, or (1) pointed. The crowns of the first upper incisors are pointed in *Brachyphylla spp.* (1). The crowns of the upper incisors of other nectar-feeding bats are not pointed (0).

40. Cingular shelf at lingual base of upper incisors—(0) absent, or (1) present. A cingular shelf is present at the lingual base of the upper incisors in *Brachyphylla spp.* (1). Other phyllostomid bats lack this structure (0).

41. Medial gap between upper incisors—(0) absent, or (1) present. A medial gap is located between the upper incisors in most of the species that have lost the lower incisors (1). It appears to be formed by a lateral migration of the upper incisors towards the canines. Only *Lichonycteris obscura* has lost the lower incisors without having a gap between the upper incisors. Two species, *Leptonycteris nivalis* and *Monophyllus redmani*, have a gap between the upper incisors, but have not lost the lower incisors. Other species do not have a gap between their upper incisors (0).

42. Shape of upper inner incisors—(0) peglike, or (1) spatulate. Spatulate incisors are flattened and expanded in the distal half of the tooth. Some members of the Lonchophyllini, such as *Platalina genovensium* and *Lonchophylla mordax*, have spatulate upper inner incisors (1), while other nectarivores have small, peg-like upper incisors (0).

43. Cusps of upper outer incisors—(0) not inflected, or (1) inflected. The crowns of

the upper outer incisors in some taxa are inflected so that the height of the crowns decreases on an angle from the crowns of the inner incisors to the gum line (1). Other species lack this inflection in their upper outer incisors, with level crowns in the same plane as the interior incisors (0).

44. Height of the crowns of the upper incisors—(0) approximately the same, or (1) inner incisors twice the height of outer incisors (Wetterer *et al.*, 2000). The upper inner incisors are more than twice the height of the outer incisors in *Brachyphylla* and *Lonchophyllini* (1). The Glossophagini all have upper incisors of roughly the same height (0).

45. Long ridge or groove on anterior face of canine—(0) absent, or (1) present. A longitudinal groove runs from near the tip of the canine to its base on the anterior face in *Monophyllus plethodon* and other taxa (1). This should not be confused with the considerable wear sometimes found on the surface of canines in many glossophagines, although dental wear sometimes makes identifying this groove difficult. Species that lack the groove are coded (0).

46. Cingulum at anterior base of upper canine—(0) absent, or (1) present. A cingular shelf is present at the anterior base of the upper canine in many nectar-feeding bats (1). Other species lack this structure (0).

47. Number of upper premolars—(2) two, or (3) three. Most nectar-feeding phyllostomid bats have two upper premolars (2). The exception is *Anoura*, with three (3).

48. Height of cusps on second upper premolar—(0) lower than canines, or (1) approximately the same as canines. The cusps on the second upper premolar reach nearly the same height as the tips of the canines in *Brachyphylla* (1). The upper premolar cusps of all other nectar-feeding phyllostomid bats are much lower than the canines (0).

49. Height of cusps on last upper premolar—(1) of equal height, (0) or middle cusp highest. In choeronycterines such as *Anoura latidens*, the three cusps on the last upper premolar are of approximately the same height (1). The middle cusp of the last upper premolar of other glossophagines is significantly higher than the two outer cusps (0).

50. Posterior cingular shelf of last upper premolar—(1) expanded, (2) shelf overlapped by trigon of M1, or (0) absent. In *Glossophaga*, *Anoura*, and *Leptonycteris*, an expanded posterior cingular shelf characterizes the labial margin of the last upper premolar (1). *Lonchophylla* also has an expanded posterior cingular shelf on the last premolar, but unlike *Glossophaga*, *Anoura*, and *Leptonycteris*, the base of this cingulum runs from the labial to lingual margins of the tooth and is overlapped by the anterior portion of the trigon of the first molar (2). Many of the glossophagines with longer rostra lack a posterior base on the last upper premolar (0).

51. Third and fourth upper premolars—(0) in contact, or (1) not in contact (Lim, 1993; Wetterer *et al.*, 2000). A space is present between the upper premolars in most glossophagines (1). The premolars are always in contact in *Brachyphylla* and other phyllostomids (0).

52. Number of upper molars—(1) one, (2) two, or (3) three. Most members of the Glossophaginae have three upper molars (3). *Leptonycteris*, *Lichonycteris*, and some *Brachyphylla nana* have two (2).

53. Hypocone and hypoconal basin on first upper molar—(0) absent, (1) present and in contact with metacone, or (2) present but not in contact with metacone (Wetterer *et al.*, 2000). The hypocone is absent on the first upper molar in most nectar-feeding phyllostomid bats (0). Other phyllostomid bats have a hypocone and a hypoconal basin; the

hypocone is in contact with the metacone (1). In *Monophyllus*, the hypocone is present, but not in contact with the metacone; it slopes toward the palate (2).

54. Parastyle on first upper molar—(0) absent, or (1) present. The parastyle on the first upper molar extends in anterior and labial directions in *Glossophaga soricina* and *Lionycteris spurelli* (1). A parastyle is absent in many taxa that have teeth similar in other respects to taxa in which the parastyle is present (0).

55. Paraconid on first lower molar—(0) absent, or (1) present (Wetterer *et al.*, 2000). The paraconid is absent on the first lower molar in Brachyphyllinae and Phyllonycterinae (1). It is present in other taxa sampled here (0).

56. Position of tips of paracone and metacone of the first upper molar—(1) shifted labially, or (0) not shifted labially. The tips of the paracone and metacone are shifted labially in Brachyphyllinae and *Platalina genovensium*, so that the greatest height of these structures is reached near the lingual margin (1). In other nectar-feeding bats, the greatest height of the paracone and metacone is in the medial region of the molar, resulting in a wide occlusal surface between the lingual margin of the molar and the tip of the metacone or paracone (e.g. *Glossophaga soricina* and *Lonchophylla thomasi*) (0).

57. Entoconid on first lower molar—(0) absent, or (1) present (Wetterer *et al.*, 2000). The entoconid is absent on the first lower molar in the Phyllonycterinae (0). Other nectar-feeding phyllostomids have an entoconid on this molar (1).

58. Styolar shelf—(1) upturned, or (0) absent. On the first upper molar of Lonchophyllini and Brachyphyllinae, the labial margin of the styolar shelf is upturned and nearly as high as the paracone and metacone on the first upper molar (1). The Glossophagini and Phyllonycterinae lack an upturned shelf (0).

59. Ectoloph on the first upper molar—(1) w-shaped, or (0) not w-shaped (Wetterer *et al.*, 2000). Most insectivorous bats have a ‘w’-shaped ectoloph on their first upper molar, suggesting that this is the ancestral condition (1). Other taxa lack the ‘w’-shaped ectoloph (0).

60. Elevation of metacone—(1) higher than paracone, or (0) subequal to paracone. The metacone is higher than the paracone on the first upper molar in *Leptonycteris* (1). In all other nectar-feeding phyllostomid bats, the paracone is at least as tall as the metacone (0). Taxa without clearly visible cusps, such as *Erophylla*, were coded (0).

61. Protocone—(1) ridge-like, or (0) not ridge-like. In the Lonchophyllini and Brachyphyllinae, the protocone on the first upper molar is a ridge-like cusp. This ridge extends along the lingual margin of the tooth and on the anterior edge inflects labially (1). Members of the Glossophagini and the Phyllonycterinae lack a ridge-like protocone (0).

62. Mesostyle—(1) prominent, or (0) not prominent. The mesostyle is a relatively large and prominent cusp on the upper molars of bats in the genera *Anoura*, *Lionycteris*, and *Lonchophylla* (1). Other nectar-feeding phyllostomid bats lack a prominent mesostyle (0).

In addition to these 62 characters of the skull, skin, and dentition, 59 characters were taken directly from Wetterer *et al.* (2000) and were not re-scored. In the remainder of this paragraph, the character description titles are reproduced from the original publication, the first number refers to the number in our data matrix (Appendix II), and the second number (in parentheses) refers to the original character number used in Wetterer *et al.* (2000).

63 (84). Third metacarpal longer than fourth or fifth (0); or third and fourth metacarpals subequal in length, both longer than fifth (1); or fourth metacarpal longest (2); or fourth and fifth metacarpals subequal in length, both longer than third (3); or third and

fifth metacarpals subequal in length, both longer than fourth (5); or third, fourth, and fifth metacarpals all subequal in length (6).

64 (85). First phalanx of digit III of wing shorter than second phalanx (0); or first and second subequal (1).

65 (86). First phalanx of digit IV of wing shorter than second phalanx (0); or subequal to second phalanx (1); or longer than second phalanx (2).

66 (90). *M. mylohyoideus* undivided (0); or partly divided into anterior and posterior parts by a fleshy aponeurosis (1); or with a pronounced break, clearly divided into distinct anterior and posterior parts (2).

67 (91). Medial fibers of *m. sternohyoideus* originate from medial manubrium (0); or from mesosternum (1); or from xiphoid process of sternum (2).

68 (92). Lateral fibers of *m. sternohyoideus* originate from manubrium (0); or from manubrium and clavicle (1); or originate from clavicle and first rib (2); or originate from xiphoid process (3).

69 (93). *M. sternohyoideus* inserts via tendon on basihyal (0); or via raphe into the fibers of *m. hyoglossus* and *m. genioglossus* (1).

70 (94). Part of *m. ceratohyoideus* inserts on ceratohyal (0); or *m. ceratohyoideus* does not insert on ceratohyal (1).

71 (95). *M. ceratohyoideus* does not insert on stylohyal (0); or part of *m. ceratohyoideus* inserts on stylohyal (1).

72 (96). *M. hyoglossus* originates via tendon from basihyal bone (0); or from raphe which forms insertion of *m. sternohyoideus* (1).

73 (97). *M. geniohyoideus* has single insertion via tendon to basihyal or basihyal raphe (0); or muscle splits near insertion, deep fibers insert directly on anterior surface of basihyal, superficial fibers insert in association with *m. hyoglossus* and *m. sternohyoideus* (1).

74 (98). Superficial fibers of *m. geniohyoideus* pass ventral to basihyal and insert into fibers of *m. hyoglossus* and *m. sternohyoideus* via raphe (0); or superficial fibers insert in well-developed loop around ventral and dorsal surfaces of the intersection of *m. hyoglossus* and *m. sternohyoideus* (1).

75 (99). Right and left *m. geniohyoideus* partly or completely fused across midline (0); or muscles not fused (1).

76 (100). *M. styloglossus* inserts on lateral surface of tongue along much of its length (0); or inserts on posterolateral "corner" of tongue (10).

77 (101). *M. genioglossus* inserts into ventral surface of tongue along more than half of its length (0); or inserts into posterior half to third of ventral surface of tongue (1); or inserts into posterior quarter of ventral surface of tongue (2).

78 (102). *M. stylohyoideus* absent (0); or present (1); or sometimes present; polymorphic within species (2).

79 (103). Anterolateral slip of *m. sphincter colli profundus* present (0); or absent (1).

80 (104). Lateral slip of *m. sphincter colli profundus* present (0); or absent (1).

81 (106). *M. cricopharyngeus* consists of a single large slip (0), or two slips (1), or three slips (2) or more than three slips (3).

82 (107). Medial circumvallate papillae present (0); or absent (1).

83 (109). Lateral circumvallate papillae present (0); or absent (1).

84 (112). Lingual sulci absent (0); or lateral lingual sulci present (1); or ventral lingual sulci present (2).

85 (113). Brush of hairlike papillae around the distal margin of the tongue absent (0); or present (1).

86 (114). Hairlike papillae confined to lateral margin of distal third of tongue, with a single line of papillae that extends roughly to LVPs (0); or hairlike papillae distributed around lateral margin and dorsum of distal third of tongue, not arranged in a single line (1).

87 (115). Hairlike papillae fleshy and conical (0); or fleshy and conical with filamentous tips (1); or cylindrical with ellipse-shaped distal end (2).

88 (117). Small patch of anteriorly directed medial-posterior mechanical papillae always absent, all papillae oriented toward pharyngeal region (0); or medial patch present in some individuals; polymorphic within species (1); or medial patch always present (2).

89 (119). Basketlike medial-posterior mechanical papillae absent (0); or present (1).

90 (120). Cluster of horny papillae located near tip of tongue (0); or located significantly proximal to tongue tip (1).

91 (124). Single large horny papilla present in center of elliptical cluster (0); or two large horny papillae present in center of elliptical cluster (1).

92 (125). Three small papillae present anterior to main papilla(e) (0); or one papilla present (1); or no papillae present (2).

93 (126). Two or more small horny papillae present posterior to main papilla(e) (0); or absent (1).

94 (127). Main horny papilla(e) flanked by a pair of smaller horny papillae, one on each side (0); or no papillae present lateral to main papilla(e) (1).

95 (128). Paired lingual arteries present, lingual veins not enlarged (0); or single, mid-line lingual artery present, lingual veins enlarged (1).

96 (135). Accessory olfactory bulb absent (0); or present (1).

97 (136). Cerebellar vermis does not cover medial longitudinal fissure or inferior colliculi (0); or cerebellar vermis completely covers longitudinal fissure between inferior colliculi, inferior colliculi exposed dorsally only along lateral edges of cerebellar vermis (1); or inferior colliculi completely covered by cerebellar vermis and cerebral hemispheres, colliculi not visible in dorsal view (2).

98 (145). Restriction site 49 present (0); or absent (1).

99 (146). Restriction site 50 present (0); or absent (1).

100 (147). Restriction site 52 present (0); or absent (1).

101 (148). Restriction site 53 present (0); or absent (1).

102 (149). Restriction site 54 present (0); or absent (1).

103 (1). Pellage differentiated into over hair and under hair (0); or pelage uniform, over hairs apparently absent (1).

104 (4). Majority of scale margins on each hair entire (0); or irregular (1); or toothed (2); or entire and irregular (3); or entire and hastate (4).

105 (5). Dorsal fur unicolored (0); or distinctly bicolored, hairs with pale bases and dark tips (1); or tricolored, hairs with distinct dark bases, a pale median band, and dark tips (2).

106 (10). Uropatagium without fringe of hair along trailing edge (0); or with distinct fringe of hair along trailing edge (1).

107 (12). Genal vibrissae absent (0); or one vibrissa present in each cluster (1), or two genal vibrissae present in each cluster (2).

108 (13). Interramal vibrissae always absent (0); or none or one interramal vibrissa

present; polymorphic within species (1); or one interramal vibrissa always present (2); or one or two interramal vibrissae present, polymorphic within species (3); or two interramal vibrissae always present (4); or none or two interramal vibrissae present; polymorphic within species (5); or three interramal vibrissae always present (6).

109 (14). Vibrissae lateral to nose/ noseleaf arranged in two columns; medial column with three or more vibrissae, lateral column with two vibrissae (0) or single column with three or more vibrissae present, lateral column absent (1).

110 (17). Padlike or flaplike vibrissal papillae not in contact across dorsum of snout (0); or pads touch, or are confluent across dorsum of snout (1).

111 (19). Noseleaf spear long, greater than twice the height of the horseshoe (0); or spear truncated, equal to or less than the height of the horseshoe (1).

112 (20). Spear of noseleaf with pointed or rounded distal tip (0); or with U-shaped notch in distal tip (1).

113 (21). Central rib absent (0); or rib restricted to proximal part of spear (1); or rib extends to distal tip of spear (2).

114 (22). Internarial region smooth, no midsagittal ridge or papillae (0); or narrow fleshy ridge or line of papillae always present along midsagittal line (1); or internarial ridge or papillae variably present; polymorphic within species (2).

115 (24). Lateral edges of horseshoe thin and free (0); or superior portion of swollen edge of horseshoe forms free, flaplike edge (1) or swollen lateral edges of horseshoe ridge-like, fused to face along entire length with no free edge (2).

116 (25). Inferior border of horseshoe is thin, free flap of skin (0); or inferior horseshoe is thickened ridge with no free edge (1); or inferior horseshoe grades smoothly into upper lip, no distinct boundary between lip and horseshoe (2).

117 (30). Chin with pair of dermal pads, one present on each side of midline (0); or chin with multiple, well-developed dermal papillae (1); or chin smooth or with a few poorly developed papillae (2); or chin partly or completely covered with skin flaps (3).

118 (32). Chin without central cleft (0); or with slight to deep central cleft (1).

119 (33). Central papillae absent from chin (0); or central dermal papilla present on chin just ventral to midline of lower lip (1).

APPENDIX II: DATA MATRIX
Skin Characters (1–3); Cranial Characters (4–19)

	1	4	6	1 1	1 6
<i>Anoura caudifer</i>	210	11	01001	01000	1200
<i>Anoura cultrata</i>	212	11	01001	01000	1200
<i>Anoura geoffroyi</i>	212	11	01001	01000	1200
<i>Anoura latidens</i>	210	11	01001	01000	1000
<i>Artibeus hirsutus</i>	112	00	00000	00000	0110
<i>Brachyphylla cavernarum</i>	122	00	00001	00000	0110
<i>Brachyphylla nana</i>	122	00	00001	00000	0110
<i>Carollia brevicauda</i>	110	00	00001	00000	1010
<i>Choeroniscus godmani</i>	110	10	01100	00100	1000
<i>Choeroniscus minor</i>	110	10	01100	00100	1000
<i>Choeroniscus periosus</i>	110	10	01100	00100	1000
<i>Choeronycteris mexicana</i>	010	10	10000	00101	1000
<i>Desmodus rotundus</i>	212	00	00001	00000	1110
<i>Erophylla bombifrons</i>	120	00	00000	00000	0101
<i>Erophylla sezekorni</i>	110	00	00000	00000	0101
<i>Glossophaga commissarisi</i>	110	10	00000	00010	1100
<i>Glossophaga leachii</i>	110	10	00001	10010	1100
<i>Glossophaga longirostris</i>	110	10	00001	00010	1100
<i>Glossophaga morenoi</i>	110	10	00001	00010	1100
<i>Glossophaga soricina</i>	110	10	00001	10010	1100
<i>Hylonycteris underwoodi</i>	110	10	00101	00010	1000
<i>Leptonycteris curasoae</i>	112	11	00001	00010	0100
<i>Leptonycteris nivalis</i>	212	11	00001	00010	0100
<i>Leptonycteris yerbabuenae</i>	112	11	00001	00010	0100
<i>Lichonycteris obscura</i>	110	01	00101	00000	0000
<i>Lionycteris spurelli</i>	110	00	00000	00000	1001
<i>Lonchophylla handleyi</i>	110	10	00000	00000	1001
<i>Lonchophylla hesperia</i>	110	10	00000	00000	1001
<i>Lonchophylla mordax</i>	110	10	00000	00000	1001
<i>Lonchophylla robusta</i>	110	10	00000	00000	1001
<i>Lonchophylla thomasi</i>	110	10	00000	00000	1001
<i>Lonchorhina aurita</i>	001	01	00000	00001	1100
<i>Macrotus californicus</i>	011	00	00001	00000	1110
<i>Monophyllus plethodon</i>	110	11	00001	00000	1100
<i>Monophyllus redmani</i>	110	11	00001	00000	1100
<i>Musonycteris harrisoni</i>	110	10	10000	00101	1000
<i>Phyllonycteris aphylla</i>	220	00	00010	00000	0001
<i>Phyllonycteris poeyi</i>	220	00	00010	00000	0001
<i>Phyllostomus discolor</i>	000	00	00000	00000	1110
<i>Platalina genovensium</i>	110	10	00000	00000	1001
<i>Pteronotus parnelli</i>	000	00	00000	00000	0110
<i>Scleronycteris ega</i>	-10	00	10000	00000	1100

APPENDIX II: DATA MATRIX
Dental Characters (20–50)

	2 0	2 6	3 1	3 6	4 1	4 6
<i>Anoura caudifer</i>	-0--10	03000	03000	00000	10101	03011
<i>Anoura cultrata</i>	-0--10	13000	03000	00000	10101	13011
<i>Anoura geoffroyi</i>	-0--10	23000	03100	00000	10101	03010
<i>Anoura latidens</i>	-0--10	03000	03100	00000	10100	03011
<i>Artibeus hirsutus</i>	020000	12000	03000	00000	00000	12000
<i>Brachyphylla cavernarum</i>	020100	12100	03000	00011	00010	12100
<i>Brachyphylla nana</i>	020100	12100	03000	00011	00010	12100
<i>Carollia brevicauda</i>	020000	12000	03000	10010	00110	02000
<i>Choeroniscus godmani</i>	-0--10	03011	03000	10000	10000	02010
<i>Choeroniscus minor</i>	-0--10	03011	03000	10000	10000	02010
<i>Choeroniscus periosus</i>	-0--10	03011	03000	10000	10000	02010
<i>Choeronycteris mexicana</i>	-0--11	13001	03000	10100	10000	02010
<i>Desmodus rotundus</i>	121000	01000	02--0	00000	00--0	00000
<i>Erophylla bombifrons</i>	020100	12000	03010	00000	00000	12000
<i>Erophylla sezekorni</i>	020100	12000	03010	00000	00000	12000
<i>Glossophaga commissarisi</i>	022111	13000	03000	00000	00100	12010
<i>Glossophaga leachii</i>	022111	13000	03000	00000	00100	12010
<i>Glossophaga longirostris</i>	022111	13000	03000	00000	00100	12010
<i>Glossophaga morenoi</i>	022111	13000	03000	00000	00100	02010
<i>Glossophaga soricina</i>	022111	13000	03000	00000	00100	12010
<i>Hylonycteris underwoodi</i>	-0--10	13000	03000	00000	10000	02010
<i>Leptonycteris curasoae</i>	020011	13000	12001	00000	00101	12011
<i>Leptonycteris nivalis</i>	120111	13000	12001	00000	10101	12011
<i>Leptonycteris yerbabuena</i>	120111	13000	12001	00000	00100	12010
<i>Lichonycteris obscura</i>	-0--00	03000	02000	10000	00000	02011
<i>Lionycteris spurelli</i>	021011	03100	03100	01000	01110	02011
<i>Lonchophylla handleyi</i>	021011	13000	03100	01000	01110	02011
<i>Lonchophylla hesperia</i>	021011	13000	03100	00000	01110	02011
<i>Lonchophylla mordax</i>	021011	13000	03100	00000	01110	02011
<i>Lonchophylla robusta</i>	021011	13000	03100	01000	01110	02011
<i>Lonchophylla thomasi</i>	021011	13000	03100	00000	01110	02011
<i>Lonchorhina aurita</i>	020001	13000	03000	01100	00110	13000
<i>Macrotus californicus</i>	020000	13000	03000	10010	00010	02001
<i>Monophyllus plethodon</i>	120110	13000	03001	10000	00101	12010
<i>Monophyllus redmani</i>	120110	13000	03001	10000	10001	12010
<i>Musonycteris harrisoni</i>	-0--11	13001	03000	10100	10000	02010
<i>Phyllonycteris aphylla</i>	020100	12000	03010	00000	00100	12000
<i>Phyllonycteris poeyi</i>	020100	12000	03010	00000	00100	12000
<i>Phyllostomus discolor</i>	020000	12000	03000	10000	00111	12001
<i>Platalina genovensium</i>	020011	13000	03000	00000	01110	02000
<i>Pteronotus parnelli</i>	02100-	13000	03000	00001	00001	12001
<i>Scleronycteris ega</i>	-0--00	13001	03001	00100	10000	02010

APPENDIX II: DATA MATRIX
Dental Characters, continued (51–62); Wing Bones (63–65)

	5 1	5 6	6 1	6 3
<i>Anoura caudifer</i>	13120	00010	01	000
<i>Anoura cultrata</i>	13100	00210	01	000
<i>Anoura geoffroyi</i>	13120	00210	01	000
<i>Anoura latidens</i>	13120	00110	01	000
<i>Artibeus hirsutus</i>	03002	-0000	00	500
<i>Brachyphylla cavernarum</i>	03102	10000	10	500
<i>Brachyphylla nana</i>	01102	10000	10	500
<i>Carollia brevicauda</i>	03100	00010	00	501
<i>Choeroniscus godmani</i>	13100	00000	00	000
<i>Choeroniscus minor</i>	13100	00000	00	000
<i>Choeroniscus periosus</i>	13100	00000	00	000
<i>Choeronycteris mexicana</i>	13100	00000	00	000
<i>Desmodus rotundus</i>	1210-	-0-00	00	401
<i>Erophylla bombifrons</i>	13102	01000	00	512
<i>Erophylla sezekorni</i>	13102	01000	00	512
<i>Glossophaga commissarisi</i>	13100	00010	00	000
<i>Glossophaga leachii</i>	13100	00010	00	000
<i>Glossophaga longirostris</i>	13100	00010	00	000
<i>Glossophaga morenoi</i>	13100	00010	00	000
<i>Glossophaga soricina</i>	13100	00010	00	000
<i>Hylonycteris underwoodi</i>	13100	00010	00	000
<i>Leptonycteris curasoae</i>	12110	00001	00	000
<i>Leptonycteris nivalis</i>	12110	00001	00	000
<i>Leptonycteris yerbabuenae</i>	12110	00001	00	000
<i>Lichonycteris obscura</i>	12100	00000	00	000
<i>Lionycteris spurelli</i>	13100	00110	10	000
<i>Lonchophylla handleyi</i>	13110	00110	10	000
<i>Lonchophylla hesperia</i>	13110	00110	10	000
<i>Lonchophylla mordax</i>	13110	00110	10	000
<i>Lonchophylla robusta</i>	13110	00110	10	000
<i>Lonchophylla thomasi</i>	13110	00110	10	000
<i>Lonchorhina aurita</i>	03011	00010	10	000
<i>Macrotus californicus</i>	13010	00011	00	402
<i>Monophyllus plethodon</i>	13210	00010	00	000
<i>Monophyllus redmani</i>	13210	00010	00	000
<i>Musonycteris harrisoni</i>	13100	00000	00	000
<i>Phyllonycteris aphylla</i>	13102	01000	00	510
<i>Phyllonycteris poeyi</i>	13102	01000	00	510
<i>Phyllostomus discolor</i>	03000	00010	01	000
<i>Platalina genovensium</i>	13100	00100	10	000
<i>Pteronotus parnelli</i>	03010	00010	10	000
<i>Scleronycteris ega</i>	13100	00001	00	000

APPENDIX II: DATA MATRIX
Hyoid Musculature (66–81); Tongue (82–95)

	6	7	7	8	8	8	9
	6	1	6	1	2	6	1
<i>Anoura caudifer</i>	0231?	1111-	12010	3	1001	11001	0?001
<i>Anoura cultrata</i>	0231?	1111-	12010	3	1001	11001	0?001
<i>Anoura geoffroyi</i>	0231?	1111-	12010	3	1001	11001	0?001
<i>Anoura latidens</i>	0231?	1111-	12010	3	1001	11001	0?001
<i>Artibeus hirsutus</i>	20100	000-1	00000	2	0000	--00	00000
<i>Brachyphylla cavernarum</i>	11200	000-?	00000	1	0100	--010	00000
<i>Brachyphylla nana</i>	11200	000-?	00000	1	0100	--010	00000
<i>Carollia brevicauda</i>	00100	000-1	00100	2	0000	--010	00000
<i>Choeroniscus godmani</i>	02310	0111?	12011	3	1001	11001	10101
<i>Choeroniscus minor</i>	02310	0111?	12011	3	1001	11001	10101
<i>Choeroniscus periosus</i>	02310	0111?	12011	3	1001	11001	10101
<i>Choeronycteris mexicana</i>	02310	0111-	12011	3	1001	11001	10101
<i>Desmodus rotundus</i>	-----	-----?	-----	-	0000	--010	-----?
<i>Erophylla bombifrons</i>	11100	000-?	00111	1	0001	12000	02001
<i>Erophylla sezekorni</i>	11100	000-?	00111	1	0001	12000	02001
<i>Glossophaga commissarisi</i>	02310	11100	12110	3	0001	11001	11121
<i>Glossophaga leachii</i>	02310	11100	12110	3	0001	11001	11121
<i>Glossophaga longirostris</i>	02310	11100	12110	3	0001	11001	11121
<i>Glossophaga morenoi</i>	02310	11100	12110	3	0001	11001	11121
<i>Glossophaga soricina</i>	02310	11100	12110	3	0001	11001	11121
<i>Hylonycteris underwoodi</i>	02310	0111?	12010	3	1001	11011	10101
<i>Leptonycteris curasoae</i>	02310	1111-	12210	3	0001	11001	11121
<i>Leptonycteris nivalis</i>	02310	1111-	12210	3	0001	11001	11121
<i>Leptonycteris yerbabuenae</i>	02310	1111-	12210	3	0001	11001	11121
<i>Lichonycteris obscura</i>	02310	0110?	12110	3	1001	11011	10101
<i>Lionycteris spurelli</i>	02310	0110?	01000	1	0011	00210	02020
<i>Lonchophylla handleyi</i>	02310	0110?	01000	1	0011	00110	02020
<i>Lonchophylla hesperia</i>	02310	0110?	01000	1	0011	00110	02020
<i>Lonchophylla mordax</i>	02310	0110?	01000	1	0011	00110	02020
<i>Lonchophylla robusta</i>	02310	0110?	01000	1	0011	00110	02020
<i>Lonchophylla thomasi</i>	02310	0110?	01000	1	0011	00110	02020
<i>Lonchorhina aurita</i>	?????	?????	?????	?	?000	--010	---??
<i>Macrotus californicus</i>	20101	100-?	00000	2	0000	--010	00000
<i>Monophyllus plethodon</i>	02310	1110?	12110	3	0001	11001	11121
<i>Monophyllus redmani</i>	02310	1110?	12110	3	0001	11001	11121
<i>Musonycteris harrisoni</i>	?????	?????	?????	?	?????	?????	?????
<i>Phyllonycteris aphylla</i>	11200	000-1	00111	1	0001	12000	02011
<i>Phyllonycteris poeyi</i>	11200	000-1	00111	1	0001	12000	02011
<i>Phyllostomus discolor</i>	20101	100-1	00000	2	0000	--010	00000
<i>Platalina genovensium</i>	02310	0110?	01000	1	0011	00200	02020
<i>Pteronotus parnelli</i>	000?0	0??-0	0?111	0	0000	---10	-----
<i>Scleronycteris ega</i>	?????	?????	?????	?	?????	?????	?????

APPENDIX II: DATA MATRIX
Brain (96–97); rDNA Restriction Sites (98–102); Pelage (103–119)

	9	9	1	1	1	1	1
	6	8	0	0	0	1	1
			1	3	6	1	6
<i>Anoura caudifer</i>	12	000	00	121	11400	00012	201-
<i>Anoura cultrata</i>	12	000	00	121	11400	00012	201-
<i>Anoura geoffroyi</i>	12	000	00	121	12400	00012	201-
<i>Anoura latidens</i>	12	000	00	121	1-400	00012	201-
<i>Artibeus hirsutus</i>	1-	000	00	121	02410	00200	0101
<i>Brachyphylla cavernarum</i>	02	000	01	001	01401	11000	2100
<i>Brachyphylla nana</i>	02	000	01	001	01401	11000	2100
<i>Carollia brevicauda</i>	12	000	00	102	00410	00110	2101
<i>Choeroniscus godmani</i>	02	101	00	101	0--00	00011	201-
<i>Choeroniscus minor</i>	02	101	00	101	00100	00011	201-
<i>Choeroniscus periosus</i>	02	101	00	101	01200	00011	201-
<i>Choeronycteris mexicana</i>	?2	101	00	101	01200	00011	201-
<i>Desmodus rotundus</i>	02	000	00	011	12400	11000	2001
<i>Erophylla bombifrons</i>	?1	???	??	001	01401	10000	201-
<i>Erophylla sezekorni</i>	?1	???	??	001	01401	10000	201-
<i>Glossophaga commissarisi</i>	12	000	00	101	00400	00012	201-
<i>Glossophaga leachii</i>	12	000	00	101	00400	00012	201-
<i>Glossophaga longirostris</i>	12	000	00	101	00400	00012	201-
<i>Glossophaga morenoi</i>	12	000	00	101	00400	00012	201-
<i>Glossophaga soricina</i>	12	000	00	101	00400	00012	201-
<i>Hylonycteris underwoodi</i>	?2	1?1	?0	102	01400	00011	201-
<i>Leptonycteris curasoae</i>	12	010	00	121	11400	00012	201-
<i>Leptonycteris nivalis</i>	12	010	00	121	11400	00012	201-
<i>Leptonycteris yerbabuena</i>	12	010	00	121	11400	00012	201-
<i>Lichonycteris obscura</i>	?2	???	??	102	01400	00011	201-
<i>Lionycteris spurelli</i>	1?	010	10	020	01600	00112	2000
<i>Lonchophylla handleyi</i>	12	010	10	101	0-600	00112	2000
<i>Lonchophylla hesperia</i>	12	010	10	101	0-600	00112	2000
<i>Lonchophylla mordax</i>	12	010	10	101	00600	00112	2000
<i>Lonchophylla robusta</i>	12	010	10	101	02600	00112	2000
<i>Lonchophylla thomasi</i>	12	010	10	101	00600	00112	2000
<i>Lonchorhina aurita</i>	?0	010	01	121	02410	00210	0000
<i>Macrotus californicus</i>	?0	000	01	101	02400	00010	1000
<i>Monophyllus plethodon</i>	12	010	00	100	00400	00012	201-
<i>Monophyllus redmani</i>	12	010	00	100	00400	00012	201-
<i>Musonycteris harrisoni</i>	??	101	00	??1	0020?	00011	201-
<i>Phyllonycteris aphylla</i>	?1	000	01	011	02401	10000	201-
<i>Phyllonycteris poeyi</i>	?1	000	01	001	02401	10000	201-
<i>Phyllostomus discolor</i>	1-	010	01	011	02010	00200	0100
<i>Platalina genovensium</i>	??	???	??	101	00600	00002	2000
<i>Pteronotus parnelli</i>	-1	---	--	040	0120-	---0-	-30-
<i>Scleronycteris ega</i>	??	???	??	??1	01?0?	00---	201-