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Phylogenetics of the Fruit-eating Bats (Phyllostomidae: Artibeina) Inferred from Mitochondrial DNA Sequences

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Abstract

Approximately 24 species classified in three groups (*Artibeus*, *Dermanura*, and *Koopmania*) compose Subtribe Artibeina, an assemblage of New World leaf-nosed bats (Phyllostomidae) for which evolutionary relationships have proven difficult to resolve. We examined artibeine systematics through broad taxonomic sampling and phylogenetic analysis of DNA sequences for two mitochondrial genes. Analysis of 16S rRNA sequences offered an additional test of previous genealogical hypotheses, and facilitated knowledge about the congruence in variation between the well studied cytochrome-*b* gene and the evolutionary history of this complex of bats. Our results illustrate a high degree of congruence between these linked mitochondrial loci that in combination offers a well resolved gene tree and robust predictions to all but a few of the examined relationships. Highlights include: monophyly of Artibeina in contrast to previous hypotheses of polyphyly; two main lineages within Artibeina in accordance with monophyly of the smaller *Dermanura* species and larger *Artibeus* species; sister relationship between *A. concolor* and other *Artibeus* species rather than with *Dermanura*, contrasting the argument for recognizing *A. concolor* as a separate genus (*Koopmania*); reconfirmation of several species formerly considered subspecies (*A. planirostris*, *A. schwartzi*, *D. bogotensis*, *D. rava*, and *D. rosenbergi*); and further indication that *A. intermedius* and *A. lituratus* are conspecific.

Key words: 16S rRNA, *Artibeus*, cytochrome-*b*, *Dermanura*, DNA sequence, *Koopmania*, phyllostomid bats, systematics

Resumen

Aproximadamente 24 especies pertenecientes a tres grupos (*Artibeus*, *Dermanura*, y *Koopmania*) componen la subtribu Artibeina, un ensamblaje de murciélagos de hoja nasal del Nuevo Mundo (Phyllostomidae), cuyas relaciones evolutivas han sido difíciles de resolver. Examinamos la sistemática de los artibeinos a través de un amplio muestreo taxonómico y análisis filogenéticos de secuencias del ADN para dos genes mitocondriales. Análisis de secuencias del gen 16S rARN ofrecen una prueba novedosa de hipótesis genealógicas previas, facilitando el conocimiento sobre la congruencia en variación respecto al mejor conocido citocromo b y la

historia evolutiva de este complejo de especies. Nuestros resultados ilustran un alto grado de congruencia entre estos loci mitocondriales, que en combinación ofrecen predicciones robustas para casi todas las relaciones examinadas. Resultados relevantes incluyen: monofilia de los Artibeina en contraste a hipótesis previas de parafilia; dos linajes mayores dentro de los Artibeina, correspondiendo con la monofilia de especies pequeñas de *Dermanura* y grandes de *Artibeus*; la relación cercana entre *A. concolor* y otras especies de *Artibeus* antes que con *Dermanura*, en contraste con la propuesta de reconocer *A. concolor* como un genero distinto (*Koopmania*); el reconocimiento de varias especies previamente consideradas subespecies (*A. planirostris*, *A. schwartzi*, *D. bogotensis*, *D. rava*, y *D. rosenbergi*); y el reconocimiento de *A. intermedius* como un sinónimo menor de *A. lituratus*.

Palabras clave: 16S rARN; *Artibeus*; citocromo-*b*; *Dermanura*; filostómidos; *Koopmania*; murciélagos; secuancias de ADN; sistemática

INTRODUCTION

Artibeine bats compose a large and diverse group of fruit-eating specialists within the New World family Phyllostomidae (subfamily Stenodermatinae: subtribe Artibeina — Baker et al. 2003). From 18 to 24 species are recognized (Simmons 2005; Larsen et al. 2007; Solari et al. in prep.) and classified into three groups: the medium- to large-sized species of *Artibeus* (*amplus*, *fimbriatus*, *fraterculus*, *hirsutus*, *inopinatus*, *intermedius*, *jamaicensis*, *lituratus*, *obscurus*, *planirostris*, and *schwartzi*), the small-sized species of *Dermanura* (*anderseni*, *azteca*, *bogotensis*, *cinerea*, *glauca*, *gnoma*, *incomitata*, *phaeotis*, *rava*, *rosenbergi*, *tolteca*, and *watsoni*); and the medium-sized *Koopmania* (*concolor*). Morphologically, *Enchisthenes hartii* shares affinities with *Artibeus* and also has been recognized as part of the artibeines (e.g., Koopman 1993, 1994).

Relationships among artibeine bats have proven difficult to resolve with the characters that have been examined so far (morphology, karyotypes, and cytochrome-*b* DNA sequences). As a result, there are disagreements over rank status of *Dermanura* and *Artibeus* and over monophyly of the group as a whole. For example, Owen's (1987, 1991) analyses of mensural and discrete-state morphological characters indicated a polyphyletic origin for Artibeina: *Artibeus* shared a most recent common ancestry with *Ectophylla* and *Uroderma* (his subtribe Artibeini) whereas *Dermanura* and *Koopmania* shared a most recent common ancestry with *Enchisthenes* and the white-shouldered stenodermatine genera (*Ametrida*, *Ardops*, *Ariteus*, *Stenoderma*, *Centurio*, *Phyllops*, *Pygoderma*, and *Sphaeronycteris*). In contrast, analyses of cytochrome-*b* DNA sequences and EcoRI-defined satellite DNA demonstrated a most recent common ancestry for *Artibeus*, *Dermanura*, and *Koopmania* (monophyly of Artibeina; Van Den Bussche et al. 1993, 1998). Based on anagenic and cladogenic interpretations of their results, coupled with morphological and karyotypic evidence (Andersen 1906; Baker 1973; Straney et al. 1979), Van Den Bussche et al. (1993, 1998) recognized *Artibeus* and *Dermanura* as separate, closely related genera, and *Koopmania concolor* as *A. concolor*. The monotypic *Enchisthenes* was regarded as genus distinct from Artibeina, which has been affirmed in additional studies of morphological and molecular data (Baker et al. 2000, 2003; Wetterer et al. 2000).

Although the Van Den Bussche et al. (1993, 1998) studies are the most important and comprehensive molecular assessments of Artibeine relationships to date, their taxonomic sampling was limited at that time by the lack of available tissue samples for *Artibeus* and *Dermanura* and lack of efficient methods of automated DNA sequencing. Tissue samples of numerous additional individuals for the taxa they examined, as well as several newly recognized species (*A. schwartzi* [Larsen et al. 2007] and *D. rava* and *D. rosenbergi* [Solari et al. in prep.]), are now available for molecular study. Also available (and feasible) now are contemporary phylogenetic methods that utilize objective systems for character weighting and efficient systems with which to reconcile important biological phenomena for molecular data (e.g., among-site rate variation, unequal base

frequencies, and nonindependence of substitutions). Therefore, our purpose in this study was to re-assess monophyly of *Artibeus*, *Dermanura*, and Artibeina, as well as the validity of *Koopmania*, through broad taxonomic sampling and phylogenetic analysis of complete cytochrome-*b* sequences along with a complementary dataset of complete 16S ribosomal RNA (rRNA) sequences. These linked genes together should increase the probability of detecting supported resolution to the gene tree (Moore 1995).

MATERIALS AND METHODS

Specimens examined.—Specimens examined are listed in the Appendix, including information associated with museum vouchers. We generated complete cytochrome-*b* sequences for 37 individuals and complete 16S rRNA sequences for 50 individuals. From GenBank, we retrieved 41 cytochrome-*b* sequences that were originally generated by Van Den Bussche et al. (1993), Lim et al. (2004), Porter and Baker (2004), Hoofer and Baker (2006), and Larsen et al. (2007), and six 16S rRNA sequences that were originally generated by Van Den Bussche and Hoofer (2000) and Baker et al. (2003). Lists of specimens examined including voucher information are accessible in each of those publications and in the Appendix. We used sequences representing *Chiroderma*, *Ectophylla*, and *Uroderma* as outgroups (Baker et al. 2000, 2003; Wetterer et al. 2000) and inferred relationships among ingroup taxa representing *Enchisthenes* and all recognized species of Artibeina excepting *D. incomitata*, for which samples were unavailable.

Molecular methods.—We extracted genomic DNA from skeletal muscle or organ tissue samples with standard phenol methods (Longmire et al. 1997). We followed previous methods to amplify and sequence the entire cytochrome-*b* (Larsen et al. 2007) and 16S rRNA (Van Den Bussche and Hoofer 2000) genes. We sequenced both strands by using Big-Dye version 3.1 chain terminators, followed by electrophoresis on a 3100-Avant Genetic Analyzer (Applied Biosystems, Foster, City, California). We assembled resulting, overlapping fragments in AssemblyLIGN™ 1.0.9 software (Oxford Molecular Group PLC, Oxford, United Kingdom) and Sequencing Analysis 3.4.1 software (Applied Biosystems, Inc., Foster City, California).

Phylogenetic analysis.—We performed multiple sequence alignment for both data sets in Clustal X software (Thompson et al. 1997) with default parameters for costs of opening and extending gaps. We viewed alignments in MacClade software (version 4.05; Maddison and Maddison 2002) to ensure there were no insertions, deletions, or stop codons in the cytochrome-*b* sequences and to inspect gap placement in the 16S rRNA sequences. We delimited ambiguously aligned sites in the 16S rRNA alignment by using criteria and justification in Hoofer and Van Den Bussche (2003), and performed data analysis without those sites. We coded nucleotides as unordered, discrete characters, gaps as missing data, and multiple states as polymorphisms. In PAUP* software (test version 4.0b10; Swofford 2002), we examined level of phylogenetic signal via the g_1-statistic (Hillis and Huelsenbeck 1992) for 100,000 randomly drawn trees.

We inferred phylogenetic relationships by Bayesian analysis implemented in MrBayes 2.01 software (Huelsenbeck and Ronquist 2001) and by Maximum Likelihood and Parsimony analyses implemented in PAUP* software (test version 4.0b10; Swofford 2002). The general time reversible (GTR) model with allowance for gamma distribution of rate variation (Γ) and for proportion of invariant sites (I) best fit both cytochrome-*b* and 16S rRNA data based on Akaike Information Criterion tests implemented in Modeltest 3.06 software (Posada and Crandall 1998).

For Bayesian analysis, we ran two X 10^6 generations with one cold and three incrementally heated Markov chains, random starting trees for each chain, and trees sampled (saved) every 100 generations. We treated model parameters as unknown variables (with uniform priors) to be estimated in each Bayesian analysis (Leaché and Reeder 2002). We ran three independent analyses with burn-in values based on empirical evaluation of likelihoods converging on stable values. We calculated a 50% majority-rule consensus tree from the sample of stabilized trees in PAUP* software (test

version 4.0b10; Swofford 2002) and obtained branch lengths via the "sumt" option in MrBayes software (Huelsenbeck and Ronquist 2001). We assessed clade reliability via posterior probabilities and regarded values ≥ 0.95 as significant.

For Maximum Likelihood analyses, we used the GTR + Γ + I model and parameters given by Modeltest (cytochrome-*b*, $r_{AC} = 2.42$, $r_{AG} = 19.70$, $r_{AT} = 2.99$, $r_{CG} = 0.69$, $r_{CT} = 41.75$, $\pi A = 0.31$, $\pi C = 0.30$, $\pi G = 0.12$, $\alpha = 1.27$, and $P_{inv} = 0.55$; 16S rRNA, $r_{AC} = 3.99$, $r_{AG} = 15.62$, $r_{AT} = 4.45$, $r_{CG} = 0.76$, $r_{CT} = 80.08$, $\pi A = 0.37$, $\pi C = 0.20$, $\pi G = 0.18$, $\alpha = 0.76$, and $P_{inv} = 0.58$), performed full heuristic searches with 10 random additions, starting trees by simple addition, tree-bisection-reconnection branch swapping, and allowance for negative branch lengths. For Parsimony analysis, we treated all characters and substitution types with equal probability and conducted full heuristic searches with 10 random additions, starting trees by simple addition, and tree-bisection-reconnection branch swapping. We assessed clade reliability via bootstrapping with 250 iterations for Parsimony analyses (Felsenstein 1985) and regarded values ≥ 70 as support. Due to computation time, we performed Maximum Likelihood bootstrapping only on the combined mitochondrial dataset and utilized a "fast" stepwise-addition approach to tree searching rather than a full-heuristic search.

RESULTS

Cytochrome-b *and 16S rRNA.*—Sequence alignment of the complete cytochrome-*b* gene for 37 specimens generated in this study (GenBank accession nos. FJ179223–FJ179259) and the 41 retrieved from GenBank was unequivocal and without internal stop codons. Of the 1,140 characters, 697 were constant and 380 parsimony-informative, with nucleotide variation distributed across codon positions as expected for protein coding genes (Simon et al. 1994): 84 at first positions, 34 at second positions, and 325 at third positions. Complete sequences of the 16S rRNA gene averaged 1,559 base pairs for the 56 taxa examined (GenBank accession nos. FJ179173–FJ179222), ranging from 1,557 (*A. fraterculus*, *A. inopinatus*, *A. schwartzi*, *D. anderseni,* and *D. cinerea*) to 1,562 (*D. watsoni*). Sequence alignment resulted in 1,578 characters, corresponding in length and similarity to other 16S rRNA sequences in GenBank. We excluded 83 characters in nine regions of the alignment (ranging from two base pairs to 46 base pairs) because of ambiguity in assessment of positional homology. This left 1,495 characters for analysis, of which 1,110 were constant and 289 parsimony-informative. Levels of phylogenetic signal were significant based on the g_1 statistic ($P < 0.01$—Hillis and Huelsenbeck 1992) for cytochrome-*b* (–0.3335) and 16S rRNA (–0.3428).

For cytochrome-*b* and 16S rRNA data sets, Bayesian likelihoods reached stationarity before 100,000 generations (i.e., burn-in = 1,000), thinning the data points to 19,000 for each data set. Topology and posterior probabilities for nodes and model parameters for all sets of runs (three runs each) within data sets agreed regardless of choice of outgroup. Maximum Likelihood analysis resulted in a single best tree for both cytochrome-*b* (Lnl = –10,611.03) and 16S rRNA (Lnl = –8,986.50) data sets. Parsimony analysis resulted in 240 most-parsimonious trees (length = 2,077, CI = 0.28, RI = 0.74) and 108 most-parsimonious trees (length = 1,125, CI = 0.46, RI = 0.77) for cytochrome-*b* and 16S rRNA data sets, respectively. For both datasets, differences among most-parsimonious trees primarily involved alternative arrangements of terminal branches within species and, in a few instances, involved alternative inter-specific relationships within *Artibeus* and *Dermanura*. Overall, there were some topological differences within and between data sets and between the three optimality criteria; however, none of the differences were supported. Statistically supported topologies (i.e., ≥ 70% bootstrap value, ≥ 0.95 Bayesian posterior probability) obtained from all optimality criteria agreed within and between each data set (Figs. 1 and 2).

Combined cytochrome-b *and 16S rRNA.*—We combined the data sets because there was high degree of congruence and no supported conflicts between them (Wiens 1998). The combined data set (2,635 base pairs) included the 49 specimens shared between data sets. It also consists of three chimeric taxa that, in both cases, included cytochrome-*b* data from one specimen and 16S rRNA data from another speci-

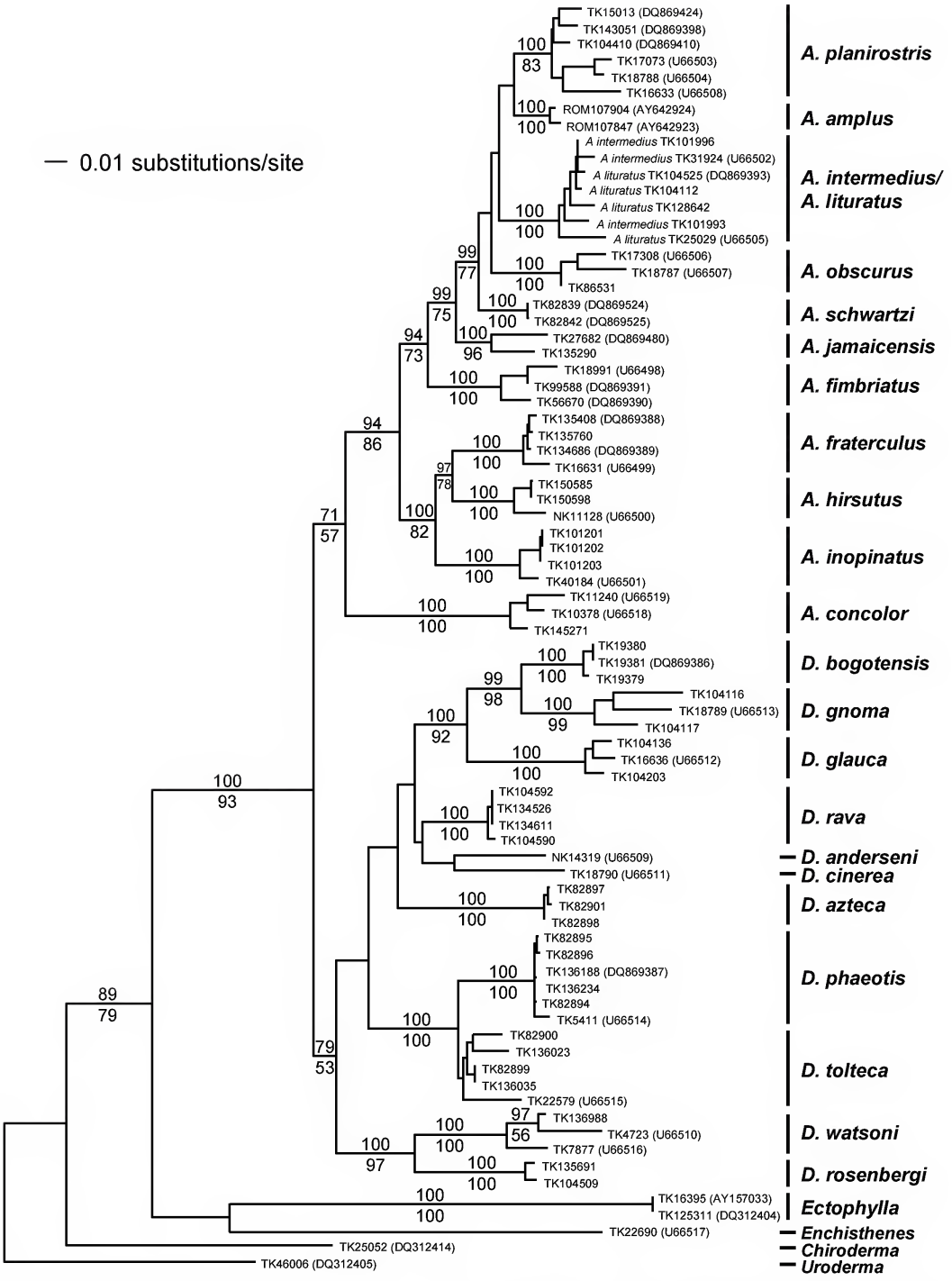

Figure 1. Maximum likelihood phylogram (Lnl = –10,611.03) from analysis of complete cytochrome-*b* sequences (1,140 base pairs) using best-fit model (GTR + Γ + I; $r_{AC} = 2.42$, $r_{AG} = 19.70$, $r_{AT} = 2.99$, $r_{CG} = 0.69$, $r_{CT} = 41.75$, $\pi A = 0.31$, $\pi C = 0.30$, $\pi G = 0.12$, $\alpha = 1.27$, and $P_{inv} = 0.55$). We designated *Chiroderma*, *Ectophylla*, and *Uroderma* as outgroups. Numbers above branches are Bayesian posterior probabilities, whereas those below are bootstrap percentages from Parsimony. Values are shown only for nodes supported by $P \geq 0.95$ or bootstrap percentage ≥ 50, or both. "*A.*" = *Artibeus,* "*D.*" = *Dermanura.*

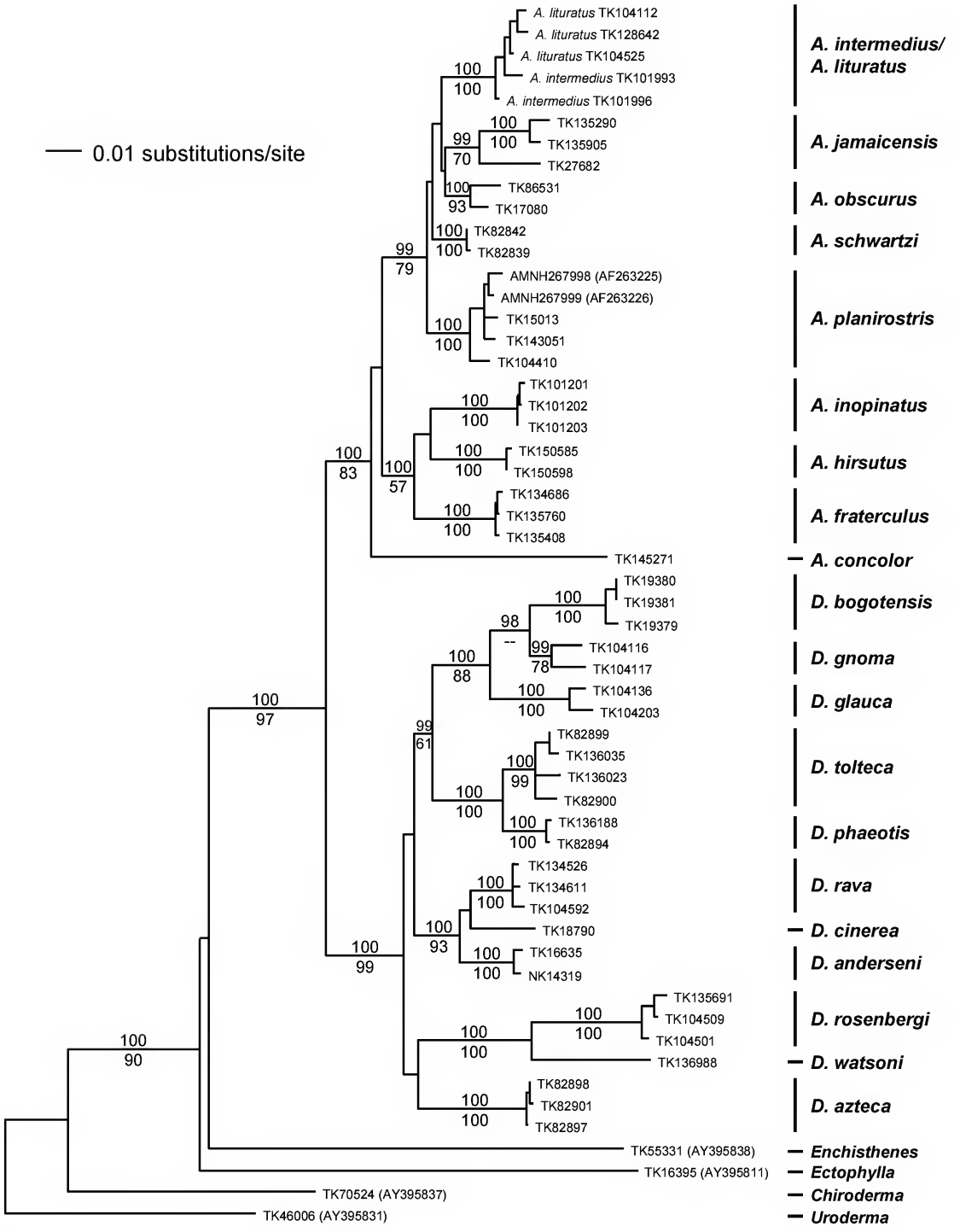

Figure 2. Maximum likelihood phylogram (Lnl = –8,986.50) from analysis of complete 16S rRNA sequences (1,495 base pairs) using best-fit model (GTR + Γ + I; $r_{AC} = 3.99$, $r_{AG} = 15.62$, $r_{AT} = 4.45$, $r_{CG} = 0.76$, $r_{CT} = 80.08$, $\pi A = 0.37$, $\pi C = 0.20$, $\pi G = 0.18$, $\alpha = 0.76$, and $P_{inv} = 0.58$). We designated *Chiroderma*, *Ectophylla*, and *Uroderma* as outgroups. Numbers above branches are Bayesian posterior probabilities, whereas those below are bootstrap percentages from Parsimony. Values are shown only for nodes supported by $P \geq 0.95$ or bootstrap percentage ≥ 50, or both. "*A.*" = *Artibeus*, "*D.*" = *Dermanura*.

men; *Artibeus obscurus* comprised two individuals, *Enchisthenes hartii* comprised two individuals, and *Chiroderma* comprised two species (*C. salvini* and *C. villosum*). Bayesian likelihoods reached stationarity before 100,000 generations as above, and topology and posterior probabilities for nodes and model parameters for all sets of runs (three runs each) agreed regardless of outgroup choice. Maximum Likelihood analysis resulted in a single best tree (Lnl= –15,882.18) and Parsimony analysis resulted in two most-parsimonious trees (length = 2,769, CI = 0.38, RI = 0.71). Topologies and levels of nodal support obtained from all three optimality criteria were nearly identical (Fig. 3).

DISCUSSION

Higher-level relationships.—Few assessments of artibeine relationships have been undertaken that included explicit phylogenetic analysis of *Enchisthenes*, *A. concolor* (= *Koopmania*), and multiple representatives of *Artibeus* and *Dermanura*. Morphological studies by Owen (1987, 1991) and molecular studies by Van Den Bussche et al. (1993, 1998) are the most comprehensive and reveal competing hypotheses of relationship. Whereas Owen's analyses of essentially all stenodermatine taxa indicate independent origins for the small- and large-sized artibeine bats, those of Van Den Bussche et al. support a recent common ancestry for these taxa after diverging from *Enchisthenes* and other stenodermatine genera. Resolving these differences is key to the higher-level systematics and taxonomy of artibeine bats.

Without Owen's hypothesis of polyphyly, which led to him to recognize genus *Artibeus* (mid- to large-sized species), elevate *Dermanura* (small-sized species) to generic rank, and describe a new genus *Koopmania* (mid-sized *A. concolor*), rank status of the three lineages within Artibeina are arbitrary. This situation has been acknowledged by several authors, as exemplified in the most recent classificatory synthesis recognizing monophyly of the group as a whole and classifying all three lineages within genus *Artibeus* (Simmons 2005). Further, the distinction of *Enchisthenes* and its distant relationship to the artibeine bats is well documented (e.g., Andersen 1906; Van Den Bussche et al. 1993; Baker et al. 2000; Wetterer et al. 2000).

Our separate and combined analyses of cytochrome-*b* and 16S rRNA sequences strongly support a clade containing all sampled individuals referable to *Artibeus*, *Dermanura*, and *Koopmania* to the exclusion of other sampled stenodermatine genera, including *Enchisthenes* (Figs. 1–3). This study therefore affirms previous cladistic analyses for supporting a recent common ancestry and monophyly of Artibeina (sensu Baker et al. 2003) in contrast to Owen's (1987, 1991) hypothesis of polyphyly. If our analyses supported the latter hypothesis, then *Artibeus* would be depicted as sharing a most recent common ancestry with *Ectophylla* and the other vampyressine genera (*Chiroderma*, and *Uroderma*), and *Dermanura* and *Koopmania* would be depicted as sharing a most recent common ancestry with *Enchisthenes*. All of our results exclude that hypothesis.

Although the phylogenetic position of *Enchisthenes* is not fully resolved, our analyses demonstrate its anagenic and cladogenic distinction relative to the artibeine bats. Thus, our results affirm previous studies of morphological, karyotypic, allozymic, and molecular data supporting the generic distinction of *Enchisthenes* (Andersen 1906, 1908; Miller 1907; Baker et al. 1979, 2000, 2003; Koop and Baker 1983; Owen 1987, 1991; Van Den Bussche 1992; Van Den Bussche et al. 1993, 1998; Pumo et al. 1996; Tandler et al. 1997; Wetterer et al. 2000) and disagree with suggestions of recognizing *E. hartii* as a congener of *Artibeus* (e.g., Koopman 1985, 1993, 1994; Jones et al. 2002). We follow Baker et al. (2003) in recognizing *E. hartii* in its own subtribe Enchisthenina separate from subtribes Artibeina, Ectophyllina, and Stenodermatina.

Within Artibeina, our analyses indicate two main lineages in accordance with monophyly of the smaller *Dermanura* species and larger *Artibeus* species. *Artibeus concolor* is sister to the large species of *Artibeus* rather than sister to *Dermanura* (Figs. 1–3). Although these relationships received different levels of statistical support in the separate analyses of cytochrome-*b* and

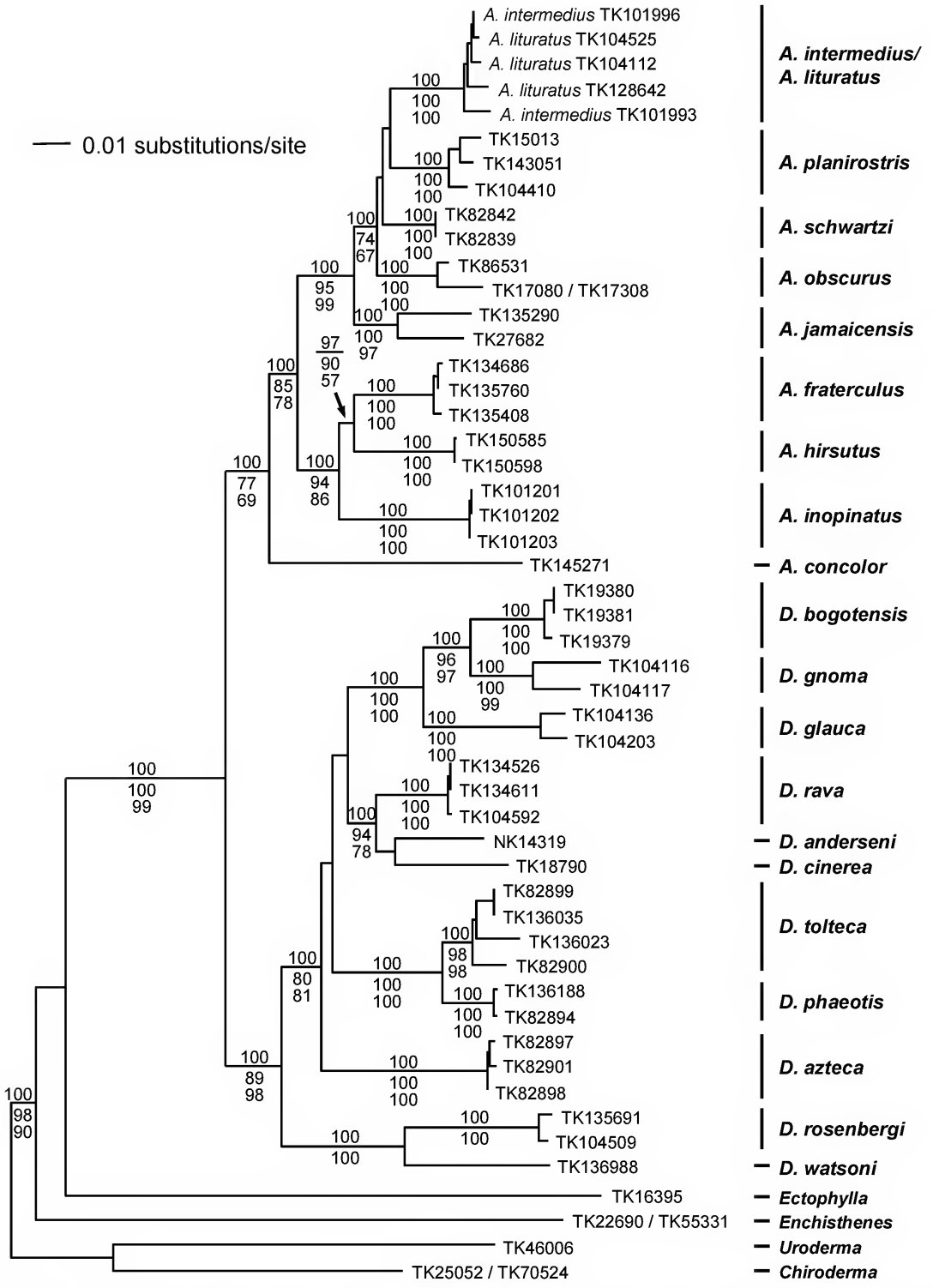

Figure 3. Maximum likelihood phylogram (Lnl = –15,882.18) from analysis of combined cytochrome-*b* and 16S rRNA sequences (2,635 base pairs) using best-fit model (GTR + Γ + I). We designated *Chiroderma*, *Ectophylla*, and *Uroderma* as outgroups. Numbers above branches are Bayesian posterior probabilities, whereas those below are bootstrap percentages from Maximum Likelihood and Parsimony, respectively. Values are shown only for nodes supported by P ≥ 0.95 or bootstrap percentage ≥ 50, or both. "*A.*" = *Artibeus*, "*D.*" = *Dermanura*.

16s rRNA sequences, they were depicted in all analyses and highly supported in the combined sequence analysis (Fig. 3). As with previous morphological, karyotypic, allozymic, and molecular evidence (Baker 1973; Straney et al. 1979; Van Den Bussche et al. 1993, 1998; Wetterer et al. 2000), our results provide no support to the objective argument of polyphyly that Owen (1991) used to justify recognizing *A. concolor* in the genus *Koopmania*. We therefore follow the suggestion of Van Den Bussche et al. (1998) and the classification of Baker et al. (2003) in recognizing *Koopmania concolor* as *Artibeus concolor*.

Although the genetic distinction and sister-taxon relationship between *Artibeus* and *Dermanura* is demonstrated in this and other studies, taxonomic status for the two lineages as subgenera within *Artibeus* or as distinct genera is a matter of subjective ranking. Several authors have discussed this issue and ranked the lineages differently (e.g., Van Den Bussche et al. 1998; Baker et al. 2000, 2003; Wetterer et al. 2000; Lim et al. 2004). Lim et al. (2004) noted that the smaller *Dermanura* species and larger *Artibeus* species cannot be diagnosed 100% on the basis of size alone because there is overlap in forearm length measurements between *D. aztecus* (41–49 mm) and two species of *Artibeus* (*concolor*, 45–51 mm; *inopinatus*, 48–53 mm). Lacking any diagnostic morphological characters, they recognized the two lineages as subgenera within *Artibeus*. Wetterer et al. (2000) also recognized them as subgenera (and *Koopmania*) within *Artibeus* because at that time there was no convenient way to refer to these taxa as a monophyletic group if generic status was applied. On the other hand, Solari et al. (2007) noted that *Artibeus* and *Dermanura* could be diagnosed on the basis of wing coloration and dental features.

We treat *Artibeus* and *Dermanura* as separate genera within the subtribe Artibeina following the classification of Baker et al. (2003). This nomenclatural arrangement facilitates convenient reference to monophyly of the group as whole, recognition of both similarities and differences within it, and additional subgeneric classification within *Artibeus* and *Dermanura* if warranted by future studies (see also Solari et al. in prep. for additional arguments). Based on our results, the latter situation seems likely after contemporary revisions are made of each genus with more data and taxa. Our arrangement also makes sense in terms of a molecular timescale of divergence of stenodermatine genera. According to Baker et al. (in litt.), *Artibeus* and *Dermanura* diverged in the Late Miocene (6.3 mya) along with most of the vampyressine genera (*Chiroderma*, *Mesophylla*, *Platyrrhinus*, *Uroderma*, *Vampyressa*, *Vampyriscus*, and *Vampyrodes*), predating the Pliocene divergence of the white-shouldered stenodermatine genera (*Ametrida*, *Ardops*, *Ariteus*, *Stenoderma*, *Centurio*, *Pygoderma*, and *Sphaeronycteris*). This divergence estimate fits the criteria for genus ranking in the Age Related Classification system proposed for Euprimate taxa (Goodman et al. 1998).

Relationships within Artibeus *and* Dermanura.—Sister group relationships and alpha taxonomy within *Artibeus* and *Dermanura* continue to be conjectural, and full revisions incorporating morphological and molecular data are warranted for both genera. Although not a primary focus of this study, the 16S rRNA data set offers robust resolution to and new insight into sister group relationships and questions of alpha taxonomy that have been debated in the morphological and cytochrome-*b* literature. We briefly discuss some of them.

Results from new cladistic analyses of morphology and cytochrome-*b* sequences, focusing on species diversity within the enigmatic *A. jamaicensis* complex, have recommended species recognition for three of the 13 subspecies within *A. jamaicensis* (Simmons 2005): *planirostris* (Patten 1971; Lim 1997; Guerrero et al. 2004; Lim et al. 2004; Larsen et al. 2007), *schwartzi* (Larsen et al. 2007); and *triomylus* (Guerrero et al. 2004; see also Larsen et al. 2007). Our analyses include specimens referable to *planirostris* and *schwartzi* (but not *triomylus*). In both cases, results from 16S rRNA analysis mirror those from cytochrome-*b* in this and other studies, yet they provide even more robust support to the branching order. Our 16S rRNA results are best interpreted as evidence for species recognition of *A. planirostris* and *A. schwartzi* as opposed to subspecies within *A. jamaicensis*. In avoiding paraphyletic taxa, the latter would require the synonymy of at least three other species within *A. jamaicensis* (*amplus*, *lituratus*, and *obscurus*). Thus, our 16S rRNA results affirm several studies of cytochrome-*b* for recognizing *A. planirostris* (Guerrero et al. 2004; Lim et al. 2004; Larsen et al. 2007), and affirm the suggestion by Larsen et al. (2007) for recognizing *A. schwartzi*.

Our mtDNA data, along with those of Larsen et al. (2007) and Lim et al. (2004), document a well supported sister relationship between the clade composed of *A. fraterculus*, *A. inopinatus*, and *A. hirsutus* and that of *A. jamaicensis*, *A. lituratus*, *A. obscurus*, *A. planirostris*, and *A. schwartzi* (Figs. 1, 2, 3). This observation has biogeographic significance, supporting the hypothesis of Patterson et al. (1992) for an historical connection between the biota of Middle America and Western Andean Slope. *Artibeus inopinatus* and *A. hirsutus* are distributed in xeric regions along the western and southern coasts of Middle America and their closest South American relative, *A. fraterculus*, is distributed in dry regions of southern Ecuador and northern Peru west of the Andes Mountains. The remaining species of *Artibeus* are sister to these xeric adapted species, and represent a South American radiation within the genus.

Results from 16S rRNA analysis also affirm previous morphological (Marques-Aguiar 1994) and cytochrome-*b* (Van Den Bussche et al. 1998; Lim et al. 2004) analyses that suggested recognizing *A. intermedius* as a junior synonym of *A. lituratus*. Average 16S rRNA sequence distance between *A. intermedius* and *A. lituratus* (0.81%) is nearly equivalent to the average distance within other *Artibeus* species (0.78%) and much less than that observed between species (4.62%). These results are of course provisional given the fact that we examined 16S rRNA sequences from just two individuals of *intermedius* (from Copan, Honduras) and three individuals of *lituratus* (from western Ecuador and Union Island, St. Vincent and the Grenadines). However, they agree with the cytochrome-*b* results from this and other studies that included more individuals. Therefore, we follow Marques-Aguiar (1994) in recognizing *A. intermedius* as a junior synonym of *A. lituratus* pending further study of combined morphological and molecular characters for populations of *intermedius* and *lituratus*, including those from the hypothesized region of sympatry in Middle America (Davis 1984; Marques-Aguiar 1994).

Even fewer cladistic analyses have been undertaken examining species diversity within *Dermanura* (morphology, Owen 1991; cytochrome-*b*, Van Den Bussche et al. 1998). A new study by Solari et al. (in prep.), incorporating both morphological and cytochrome-*b* analyses and dense taxonomic and geographic sampling, recommended species recognition for *D. bogotensis* and *D. rosenbergi*, former junior synonyms of *D. glauca*, and species recognition for *D. rava*, a former junior synonym of *D. phaeotis*. Our analyses include specimens referable to all of these taxa. In each case, our results from 16S rRNA analysis mirror those from cytochrome-*b* in this study and Solari et al. (in prep.), supporting a sister relationship between *D. bogotensis* and *D. gnoma*, another between *D. rosenbergi* and *D. watsoni*, and a clade containing *D. rava*, *D. anderseni*, and *D. cinerea*. Our 16S rRNA results are best interpreted as evidence for species recognition of *D. bogotensis* and *D. rosenbergi*, rather than junior synonyms of *D. glauca*, and species recognition for *D. rava*, rather than a junior synonym of *D. phaeotis*. To avoid paraphyletic taxa, the alternative classification (Simmons 2005) would require synonymizing from one to nine other species and major taxonomic rearrangement. Thus, we follow Solari et al. (in prep.) in recognizing 12 species within *Dermanura*, the nine listed in Simmons (2005; we did not sample *incomitata*) plus *D. bogotensis*, *D. rava*, and *D. rosenbergi*.

Our hypotheses of relationship for species diversity and species groups within *Dermanura* depart significantly from previous hypotheses for the genus, including Handley (1987). Like cytochrome-*b*, our 16S rRNA results correspond with geographic origin of *Dermanura* species better than with morphological similarity. Accordingly, we conclude that our systematic and taxonomic hypotheses better reflect actual phyletic relationships rather than adaptive similarity. This is evidenced by biogeographic patterns in the *Dermanura* phylogeny that correspond well with diversification patterns hypothesized for *Artibeus* as well as other vertebrates (see Solari et al. in prep. for discussion of *Dermanura* phylogeography).

In summary, our phylogenetic analysis of cytochrome-*b* data includes fairly dense and complete taxonomic sampling for both genera and most recognized species within them. More importantly, analysis of 16S rRNA sequences offers a new test of previous hypotheses about shared common ancestry, sister group relationships, and alpha taxonomy, thereby facilitating knowledge about the congruence in variation between the well studied cytochrome-*b* gene and the evolutionary history of bats within *Artibeus* and *Dermanura*. Our results illustrate a high degree of congruence between

these linked mitochondrial loci that in combination offer a well-resolved gene tree and robust predictions to all but a few of the examined relationships (Fig. 3). Testing the mtDNA phylogeny with independent nuclear gene sequences and broad taxonomic sampling are highly desirable to further advance our understanding of the systematics and taxonomy of artibeine bats.

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APPENDIX

List of specimens examined, including geographic locality, tissue and voucher numbers, and GenBank accession numbers for cytochrome-*b* and 16S rRNA sequences. Asterisks (*) by GenBank accession numbers denote sequences generated in this study. Voucher specimens are housed in the following institutions: American Museum of Natural History (AMNH); Carnegie Museum of Natural History (CM); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Peru (MUSM); Museum of Southwestern Biology, University of New Mexico (MSB); Museum of Texas Tech University (TTU); Museum of Vertebrate Zoology, Berkeley (MVZ); Royal Ontario Museum (ROM); and United States National Museum of Natural History (USNM). Museum catalog numbers are missing for vouchers that are housed but not yet cataloged or the number is unknown.

Taxon	Locality	Tissue no.	Voucher no.	Accession no. Cyt-b	16S
Artibeus amplus	VENEZUELA: Amazonas	ROM 107904	ROM 107904	AY642924	———
	VENEZUELA: Amazonas	ROM 107847	ROM 107847	AY642923	———
A. concolor	SURINAME: Brokopondo	TK 10378	CM 63792	U66518	———
	SURINAME: Brokopondo	TK 11240	CM 63789	U66519	———
	SURINAME: Sipallawinie	TK 145271	TTU 104508	FJ179223	FJ179173
A. fimbriatus	BRAZIL: Sao Paulo	TK 18991	———	U66498	———
	PARAGUAY: San Pedro	TK 99588	TTU 96431	DQ869391	———
	PARAGUAY: Canindeyu	TK 56670	TTU 94457	DQ869390	———
A. fraterculus	PERU: Lambayeque	TK 16631	MVZ 168913	U66499	———
	ECUADOR: Guayas	TK 134686	TTU 130519	DQ869389	FJ179174
	ECUADOR: El Oro	TK 135408	TTU 102476	DQ869388	FJ179175
	ECUADOR: El Oro	TK 135760	TTU 102814	FJ179224	FJ179176
A. hirsutus	MEXICO: Sonora	NK 11128	MSB 54923	U66500	———
	MEXICO: Michoacan	TK 150585	TTU 104509	FJ179225	FJ179180
	MEXICO: Michoacan	TK 150598	TTU 104510	FJ179226	FJ179181
A. inopinatus	HONDURAS: Valle	TK 40184	TTU 61115	U66501	———
	HONDURAS: Valle	TK 101201	TTU 83862	FJ179227	FJ179177
	HONDURAS: Valle	TK 101202	TTU 83863	FJ179228	FJ179178
	HONDURAS: Valle	TK 101203	TTU 83864	FJ179229	FJ179179
A. intermedius	COSTA RICA: Guanacaste	TK 31924	———	U66502	———
	HONDURAS: Copan	TK 101993	TTU 84650	FJ179230	FJ179182
	HONDURAS: Copan	TK 101996	TTU 84653	FJ179231	FJ179183
A. jamaicensis	JAMAICA: St. Anns	TK 27682	TTU 45295	DQ869480	FJ179187
	ECUADOR: Loja	TK 135290	TTU 103794	FJ179232	FJ179186
	ECUADOR: Esmeraldas	TK 135905	TTU 103109	———	FJ179188

APPENDIX (CONT.)

A. lituratus	TRINIDAD & TOBAGO: Trinidad	TK 25029	———	U66505	———
	ECUADOR: Pastaza	TK 104112	TTU 84884	FJ179233	FJ179194
	ECUADOR: Esmeraldas	TK 104525	TTU 85297	DQ869393	FJ179195
	ST. VINCENT AND THE GRENADINES: Union Island	TK 128642	TTU 104511	FJ179234	FJ179196
A. obscurus	SURINAME: Nickerie	TK 17080	CM 68951	———	FJ179185
	SURINAME: Para	TK 17308	TTU 35725	U66506	———
	FRENCH GUIANA: Sinnamary	TK 18787	AMNH 267210	U66507	———
	GUYANA: N.W. District	TK 86531	———	FJ179235	FJ179184
A. planirostris	FRENCH GUIANA: Sinnamary	AMNH 267998	AMNH 267998	———	AF263225
	FRENCH GUIANA: Sinnamary	AMNH 267999	AMNH 267999	———	AF263226
	VENEZUELA: Guarico	TK 15013	TTU 33333	DQ869424	FJ179189
	PERU: Madre de Dios	TK 16633	MVZ 170016	U66508	———
	SURINAME: Nickerie	TK 17073	CM 68950	U66503	———
	FRENCH GUIANA: Sinnamary	TK 18788	AMNH 267202	U66504	———
	ECUADOR: Pastaza	TK 104410	TTU 85182	DQ869410	FJ179191
	FRENCH GUIANA: Remire-Montjoly	TK 143051	CM 83901	DQ869398	FJ179190
A. schwartzi	ST. VINCENT AND THE GRENADINES: St. Vincent	TK 82839	CM 83210	DQ869524	FJ179193
	ST. VINCENT AND THE GRENADINES: St. Vincent	TK 82842	CM 83218	DQ869525	FJ179192
Chiroderma villosum	TRINIDAD & TOBAGO: Trinidad	TK 25052	CM 97374	DQ312414	———
C. salvini	PERU: Cusco	TK 70524	MUSM 13611	———	AY395837
Dermanura anderseni	BOLIVIA: Pando	NK 14319	MSB 57026	U66509	FJ179198
	PERU: Madre de Dios	TK 16635	MVZ 166563	———	FJ179197
D. azteca	MEXICO: Morelos	TK 82897	———	FJ179236	FJ179199
	MEXICO: Queretaro	TK 82898	———	FJ179237	FJ179200
	MEXICO: Queretaro	TK 82901	———	FJ179238	FJ179201
D. bogotensis	VENEZUELA: Merida	TK 19379	CM 78457	FJ179239	FJ179202
	VENEZUELA: Merida	TK 19380	CM 78458	FJ179240	FJ179203
	VENEZUELA: Merida	TK 19381	CM 78459	DQ869386	FJ179204
D. cinerea	FRENCH GUIANA: Sinnamary	TK 18790	AMNH 267197	U66511	FJ179222
D. glauca	PERU: Cusco	TK 16636	MVZ 173952	U66512	———
	ECUADOR: Pastaza	TK 104136	TTU 84908	FJ179241	FJ179206
	ECUADOR: Tungurahua	TK 104203	TTU 84975	FJ179242	FJ179207
D. gnoma	FRENCH GUIANA: Sinnamary	TK 18789	AMNH 267200	U66513	———
	ECUADOR: Pastaza	TK 104116	TTU 84888	FJ179243	FJ179208
	ECUADOR: Pastaza	TK 104117	TTU 84889	FJ179244	FJ179209
D. phaeotis	NICARAGUA: Managua	TK 5411	TTU 30513	U66514	———
	MEXICO: Chiapas	TK 82894	———	FJ179245	FJ179218
	MEXICO: Guerrero	TK 82895	———	FJ179246	———
	MEXICO: Tabasco	TK 82896	———	FJ179247	———
	HONDURAS: Atlantida	TK 136188	TTU 103810	DQ869387	FJ179217
	HONDURAS: Colon	TK 136234	TTU 104100	FJ179248	———
D. rava	ECUADOR: Esmeraldas	TK 104590	TTU 85362	FJ179249	———
	ECUADOR: Esmeraldas	TK 104592	TTU 85364	FJ179250	FJ179212
	ECUADOR: Guayas	TK 134526	TTU 103616	FJ179251	FJ179210
	ECUADOR: Guayas	TK 134611	TTU 103701	FJ179252	FJ179211
D. rosenbergi	ECUADOR: Esmeraldas	TK 104501	TTU 85273	———	FJ179220
	ECUADOR: Esmeraldas	TK 104509	TTU 85281	FJ179253	FJ179221
	ECUADOR: Esmeraldas	TK 135691	TTU 103170	FJ179254	FJ179219
D. tolteca	PANAMA: Darien	TK 22579	———	U66515	———
	MEXICO: Chiapas	TK 82899	———	FJ179255	FJ179213
	MEXICO: Morelos	TK 82900	———	FJ179256	FJ179215
	HONDURAS: Comayagua	TK 136023	TTU 104294	FJ179257	FJ179214
	HONDURAS: Comayagua	TK 136035	TTU 104306	FJ179258	FJ179216
D. watsoni	MEXICO: Sinaloa	TK 4723	TTU 35568	U66510	———
	NICARAGUA: Zelaya	TK 7877	TTU 30536	U66516	———
	HONDURAS: Colon	TK 136988	TTU 104077	FJ179259	FJ179205
Ectophylla alba	COSTA RICA: Limon	TK 16395	ROM 108296	AY157033	AY395811
	COSTA RICA: Limon	TK 125311	USNM 568512	DQ312404	———
Enchisthenes hartii	PERU: Huanuco	TK 22690	CM 98710	U66517	———
	PERU: Cusco	TK 55331	USNM 582822	———	AY395838
Uroderma magnirostrum	EL SALVADOR: San Miguel	TK 46006	TTU 62670	DQ312405	AY395831

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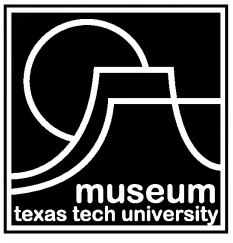

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