6-1-2007

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Journal of Mammalogy, 88(3):712–727, 2007

PHYLOGENETICS AND PHYLOGEOGRAPHY OF THE *ARTIBEUS JAMAICENSIS* COMPLEX BASED ON CYTOCHROME-*b* DNA SEQUENCES

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The phylogenetics and phylogeography of the Jamaican fruit-eating bat (*Artibeus jamaicensis*) were examined based on analysis of DNA sequence variation in the mitochondrial cytochrome-*b* gene for 176 individuals representing all 13 subspecies of *A. jamaicensis* (sensu Simmons 2005). Results document that *A. jamaicensis* (sensu Simmons 2005) comprises 3 monophyletic assemblages that are separated phylogenetically by the presence of *A. obscurus*, *A. lituratus*, and *A. amplus*. According to the mitochondrial DNA sequence variation, *A. jamaicensis*, *A. schwartzi*, and *A. planirostris* are appropriate species-level names for these lineages. Haplotypes identifiable as *A. jamaicensis* were absent east of the Andes Mountains in South America; haplotypes of *A. schwartzi* were documented throughout the Lesser Antilles and from northern Venezuela, and haplotypes of *A. planirostris* were identified east of the Andes Mountains in South America, north of the Orinoco River in Venezuela, and from the southern Lesser Antilles. Haplotypes of *Artibeus jamaicensis*, *A. schwartzi*, and *A. planirostris* were identified sympatrically on Carriacou, a small island in the southern Lesser Antilles that is ecologically monotypic. The magnitude of genetic divergence separating *A. jamaicensis*, *A. planirostris*, and *A. schwartzi* essentially equals the magnitude of genetic divergence distinguishing *A. lituratus*, *A. obscurus*, and *A. jamaicensis*. Studies of the nuclear genome will be required to understand the biological implications of these patterns in the mitochondrial genome.

Key words: *Artibeus jamaicensis*, cytochrome *b*, mitochondrial DNA, phylogenetics, phylogeography, phylogroups, species, Genetic Species Concept

The Jamaican fruit-eating bat, *Artibeus jamaicensis* (Leach, 1821), is one of the most common and well-studied neotropical mammals. It has been a model organism in a wide array of research projects on or about cell structure and function, the mitochondrial genome, ecology, physiology, conservation, behavior, and biogeography (e.g., Fleming 1971; Handley et al. 1991a, 1991b; Ortega and Arita 1999; Pumo et al. 1998; Studier and Wilson 1991; Tandler et al. 1986). However, despite this research interest in the Jamaican fruit-eating bat, fundamental questions about its distribution, phylogeny, systematics, and even species definition remain a century-old debate (Table 1).

The debate regarding *A. jamaicensis* (sensu Simmons 2005) stems from difficulties in resolving phylogenetic and classification issues with traditional morphological criteria. The significance of phenotypic variation in size, color, and dentition across the species' geographic and ecologic range has undergone multiple interpretations (Table 1). Until now, the molecular systematics of *A. jamaicensis* (sensu Simmons 2005) has not been examined.

Thirteen subspecies of *A. jamaicensis* are recognized in the most recent taxonomic synthesis (Simmons 2005): *aequatorialis*, *fallax*, *grenadensis*, *hercules*, *jamaicensis*, *parvipes*, *paulus*, *planirostris*, *richardsoni*, *schwartzi*, *trinitatis*, *triomylus*, and *yucatanicus* (Fig. 1). However, at least 3 of these might be species. Specimens of *Artibeus* "*jamaicensis*" from east of

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TABLE 1.—Historically recognized subspecies that have been placed in *Artibeus jamaicensis* in selected previous publications. ● = subspecies recognized in *A. jamaicensis*; ○ = taxon recognized as a species distinct from *A. jamaicensis*; P = subspecies of *A. planirostris*; L = subspecies of *A. lituratus*; X1 = synonym of *trinitatis*; X2 = synonym of *jamaicensis*. *Artibeus obscurus* (sensu Handley 1989) = *A. davisi* of Patten (1971) and *A. fuliginosus* of Tuttle (1970) and previous authors.

Selected Accounts	*aequatorialis*	*fallax*	*fraterculus*	*grenadensis*	*hercules*	*lituratus*	*obscurus*	*palmarum*	*parvipes*	*paulus*	*planirostris*	*praeceps*	*richardsoni*	*schwartzi*	*trinitatis*	*triomylus*	*yucatanicus*
Andersen (1908)	●	P		P		●		●	●		○	●			P		●
Hershkovitz (1949)	L	L	●	X1		○		L	●		●	L	X2		●		●
Koopman (1968)						○		L			●	X2			●		
Jones and Phillips (1970)				X1				L			●			●	●		
Davis (1970)						○				●			●			●	●
Patten (1971)	●	P	○			○	○				○		●		●		
Jones and Carter (1976)		L	●		L	○		L	●	●	●		●		●	●	●
Koopman (1978)		P	○		P	○	○								●		
Hall (1981)						○			●				●		●	●	●
Honaki et al. (1982)		P	○		P	○	○	L			○	●			●		
Handley (1987)	●	●			●	○	○				○				●		
Koopman (1994)*	●	P	○		P	○	●	L	●	●	○		●	●	●	●	●
Koopman (1993)	●	P	○	●	P	○	○	L	●	●	○		●	●	●	●	●
Marques-Aguiar (1994)	●	●	○		●	○	○	L	●	●	●		●	●	●	●	●
Genoways et al. (1998)				●										●	●		
Ortega and Castro-Arellano (2001)									●	●			●		●	●	●
Guerrero et al. (2004)		P				○	○			●	○		●			○	●
Simmons (2005)	●	●	○	●	●	○	○	L	●	●	●		●	●	●	●	●
This paper	●	P	○	P	P	○	○	L	●	●	○		●	○	P	●	●

[a] Koopman (1994): Chiroptera chapter completed in 1988 and published largely unrevised 6 years later in 1994.

the Andes Mountains and south of the Orinoco River in South America (*planirostris*), west of the Sierra Madre Mountains in southern Mexico (*triomylus*), and the southern Lesser Antillean island of St. Vincent (*schwartzi*) all have been hypothesized as different species based on morphological or molecular studies, or both (Andersen 1908; Guerrero et al. 2004; Lim 1997; Lim and Wilson 1993; Lim et al. 2004; Patten 1971; Phillips et al. 1989). Thus, the definition of *A. jamaicensis* and its distributional limits remain unclear.

The objective of the present study was to examine the phylogenetics and phylogeography of the *A. jamaicensis* complex based on DNA sequence variation in the mitochondrial cytochrome-*b* gene. Species boundaries are best defined by the nuclear genome, but interpretation of the variation of a protein-coding mitochondrial gene will provide a basis to understand data from the nuclear genome and morphology.

MATERIALS AND METHODS

Specimens examined.—Tissues were collected from natural populations and archived, by freezing or suspension in lysis buffer, in the following institutions: Natural Science Research Laboratory, Museum of Texas Tech University; Museo de Zoologia, Pontificia Universidad Católica del Ecuador; and Hofstra University. All animals were handled following the guidelines for animal care and use established by the American Society of Mammalogists (Animal Care and Use Committee 1998). Specimens were initially identified using museum voucher records, geographic collecting localities, or both within the defined subspecific ranges of *A. jamaicensis* (sensu Simmons 2005; Fig. 1).

Molecular methods.—Total genomic DNA was extracted from liver or skeletal muscle tissues for 143 individuals by using

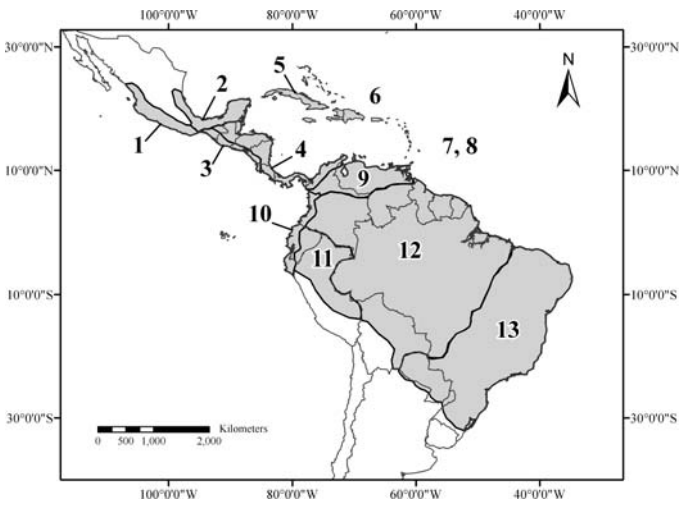

FIG. 1.—Geographic distribution of the *Artibeus jamaicensis* complex (sensu Simmons 2005). 1 = *triomylus*, 2 = *yucatanicus*, 3 = *paulus*, 4 = *richardsoni*, 5 = *parvipes* (Cuba), 6 = *jamaicensis* (Jamaica, east and south to Barbados), 7 = *schwartzi* (St. Vincent), 8 = *grenadensis* (Grenada), 9 = *trinitatis*, 10 = *aequatorialis*, 11 = *hercules*, 12 = *fallax*, and 13 = *planirostris*. Modified from Davis (1970), Eisenberg (1989), Koopman (1982), Lim (1997), Patten (1971), and Redford and Eisenberg (1992).

either phenol–chloroform methods (Longmire et al. 1997) or the DNeasy Tissue Kit (Qiagen Inc., Valencia, California). The entire cytochrome-*b* gene was amplified by the polymerase chain reaction (Saiki et al. 1988) with the flanking primers G6H and G7L (Hoffmann and Baker 2001) using a 50-µl reaction, approximately 400 ng DNA, 0.30 µM each primer, 1.25 mM $MgCl_2$, 0.2 mM deoxynucleoside triphosphates, 1X reaction buffer, and 1.25U *Taq* DNA polymerase (Promega Corporation, Madison, Wisconsin). The reactants were heated at 94°C for 2 min, then amplified for 34 cycles of denaturation at 94°C for 40 s, annealing at 53°C for 40 s extension at 72°C for 1 min, followed by 72°C for 15 min. Polymerase chain reaction products were purified using the QIAquick PCR Purification Kit (Qiagen Inc., Chatsworth, California).

Following manufacturer's recommendations, DNA sequencing was performed using ABI Big Dye chemistry chain terminators version 3.1 and fragments were electrophoresed on an ABI 3100-*Avant* Genetic Analyzer (PE Applied Biosystems, Foster City, California). The 2 external primers and 4 internal primers (G1L and G5L—Hoffmann and Baker 2001; MVZ04—Smith and Patton 1993; ART16 [5′-ATR-TAA-TTR-TCT-GGG-TCT-CC-3′]), were used to sequence the entire 1,140 base pair gene in both directions. For each animal, sequences from each primer were verified and assembled using the Vector NTI 9.0 software suite (InforMax Frederick, Maryland). To ensure correct open-reading frame, multiple sequence alignment was performed manually and further checked in MacClade software version 4.05 (Maddison and Maddison 2000).

Phylogenetic analyses.—Phylogenetic analyses were performed in MrBayes software, version 2.01 (Huelsenbeck and Ronquist 2001) and PAUP software, version 4.0b10 (Swofford 2002). Minimum-evolution, maximum-likelihood, maximum-parsimony (unweighted), and Bayesian analysis were used to infer phylogenies. The general time reversible (GTR) model of substitution with allowance for gamma distribution (Γ) of rate variation and for proportion of invariant sites (I) best fit the data (Modeltest—Posada and Crandall 1998), and was used in minimum-evolution and maximum-likelihood analyses with full heuristic searches using neighbor-joining starting trees and tree-bisection-reconnection branch swapping. Maximum parsimony was performed using heuristic searches, 25 replicates of the random taxon addition option, each with random starting trees, and tree-bisection-reconnection branch-swapping. For bootstrap support values, 250 replicates were conducted using the heuristic search criterion. Phylogenetic relationships and posterior probabilities were generated using Bayesian analysis, which was run with 4 Monte Carlo chains for 1 million generations. Three separate Bayesian analyses were performed with alternative outgroup choices and trees were sampled every 100 generations with a burn-in value of 1,000 trees. Genetic distances using the Kimura 2-parameter model were generated in MEGA software (Kumar et al. 2004) to allow for comparisons with other molecular studies of *Artibeus* and other mammals (Bradley and Baker 2001; Guerrero et al. 2004; Lim et al. 2004). Unique haplotypes were identified by analysis with Collapse software, version 1.2 (Posada 2004).

Sequences of *Koopmania concolor*, *Dermanura bogotensis*, and *D. phaeotis* were chosen as outgroups because previous morphological and molecular studies agree that these taxa are outgroups to *Artibeus* (Baker et al. 2003; Owen 1987; Van Den Bussche et al. 1998; Wetterer et al. 2000). Cytochrome-*b* sequences of 33 specimens from Davalos and Jansa (2004), Guerrero et al. (2004), J. A. Guerrero et al. (pers. comm.), Lim et al. (2004), and Van Den Bussche et al. (1998) were obtained from GenBank (accession numbers given in Appendix I) and included in analyses.

Results

The entire cytochrome-*b* gene (1,140 base pairs) was sequenced for 143 specimens and submitted to GenBank (Appendix I). Alignment of these sequences plus the 33 from GenBank was unequivocal and without internal stop codons. A total of 176 specimens was examined, of which 104 unique haplotypes were identified. Identical sequences were excluded from some analyses to prevent repetitive sampling and to minimize computational time. Of 1,140 characters, 780 were invariant, and 272 were parsimony informative. Including outgroups, 32 of the informative characters were at 1st codon positions, 11 at 2nd positions, and 229 at 3rd positions. Initially, relationships within and among species of *Artibeus* were examined using Bayesian analyses of all unique haplotypes (Fig. 2). Three distinct clades, referred to as clades A, B, and C (Fig. 2), were identified within *A. jamaicensis* (sensu Simmons 2005).

Diversity within species was identified and the data set was then truncated to 57 operational taxonomic units to elucidate intrageneric relationships. Of the 1,140 characters, 795 were constant and 85 were autapomorphic, leaving 260 parsimony-informative characters. Twenty-eight of the informative characters were at the 1st position, 10 at the 2nd position, and 222 at the 3rd position. Parsimony analysis generated 72 most-parsimonious trees of 1,008 steps (retention index = 0.751, consistency index = 0.403). Topology of the strict consensus of the 72 equally parsimonious trees was similar to trees generated in all analyses. Maximum likelihood resulted in 1 tree with a –ln-likelihood (−lnL) of 6,326.17 (Fig. 3) and minimum evolution resulted in a single least-evolved tree with a score of 0.93. Supported relationships were identical in each analysis. Average genetic distances between species of *Artibeus* (Table 2) ranged from 4.1% (*A. amplus* versus clade C of *A. jamaicensis*) to 9.3% (*A. fraterculus* versus clade C of *A. jamaicensis*).

Variation within A. jamaicensis.—In all analyses, *A. jamaicensis* (sensu Simmons 2005) was polyphyletic (Figs. 2 and 3). The average Kimura 2-parameter distance for all pairwise comparisons within the *A. jamaicensis* complex was 4.3%. Average distances ranged from 0.0% (*jamaicensis*) to 1.9% (*fallax*; Table 3) within subspecies, and from 7.5% (*planirostris* versus *paulus* and *hercules* versus *paulus*) to 0.1% (*parvipes* versus *jamaicensis*; Table 3) between subspecies.

Clade A includes 88 specimens collected from Ecuador (west of the Andes Mountains), Central America, Mexico, and the Caribbean (Fig. 4), representing the subspecies *aequatorialis*

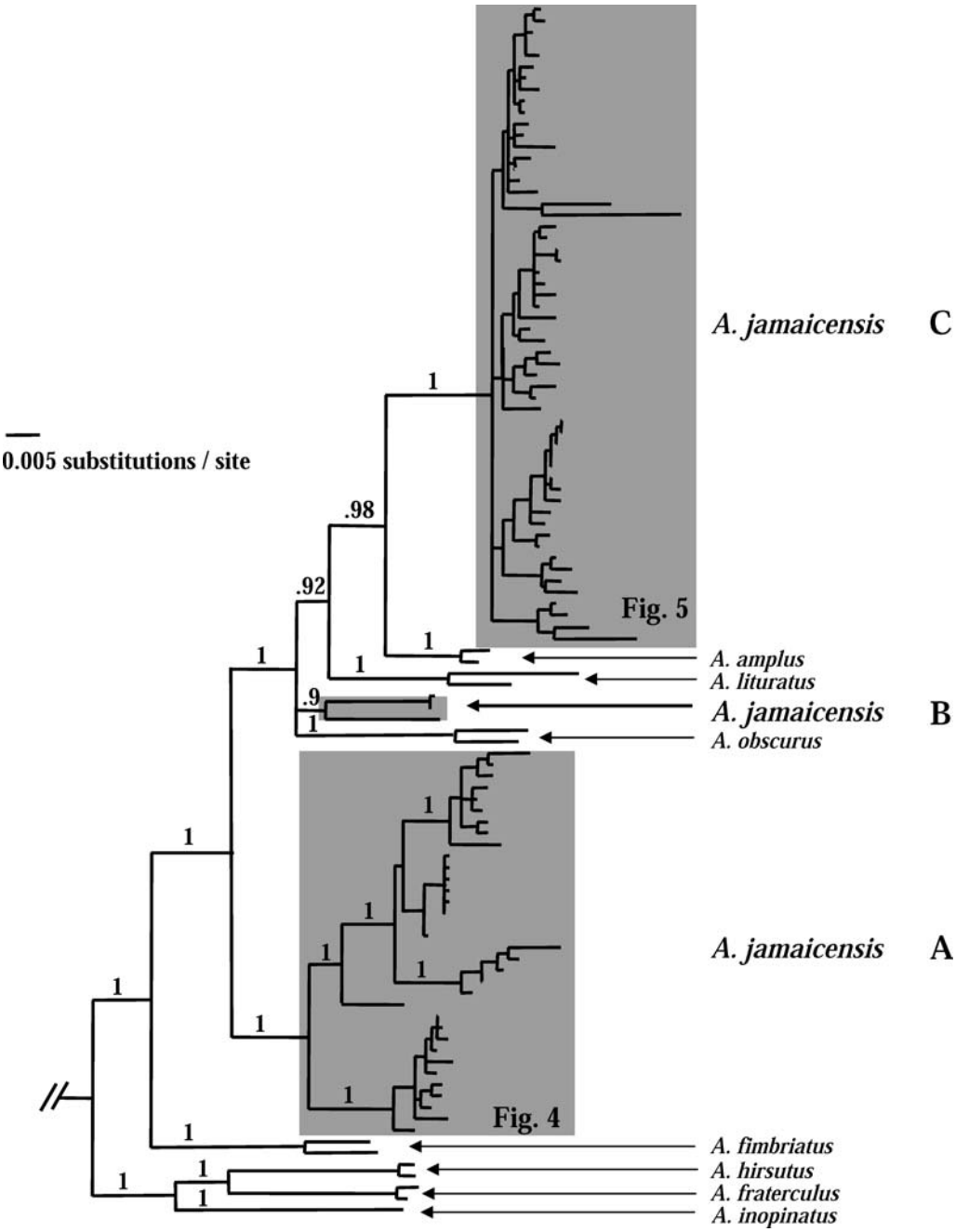

Fig. 2.—Bayesian phylogram (−lnL = 8,048.48) based on unique haplotypes of DNA sequences of the entire cytochrome-*b* gene and GTR+Γ+I model of evolution. Bayesian posterior probabilities are shown above each branch. All nodes are shown with ≥0.9 posterior probabilities also were recovered in strict consensus trees from both maximum parsimony and minimum evolution. *Koopmania concolor*, *Dermanura bogotensis*, and *D. phaeotis* were used as outgroups but are not shown. Shaded clades represent the *A. jamaicensis* complex (sensu Simmons 2005). Clades A and C are shown in detail in Figs. 4 and 5.

($n = 11$), *richardsoni* ($n = 6$), *parvipes* ($n = 1$), *paulus* ($n = 3$), *triomylus* ($n = 5$), *yucatanicus* ($n = 6$), and *jamaicensis* ($n = 56$). Thirty-five haplotypes were identified within clade A. Genetic distances between members of clades A and B and clades A and C averaged 6.1% and 6.8%, respectively (Table 2). Average genetic distances within clades A, B, and C were 3.0%, 2.5%, and 1.7%, respectively.

Clade B includes 13 specimens collected from Montserrat, Nevis, St. Kitts, St. Vincent, Carriacou, and Venezuela south of Lake Maracaibo, representing the subspecies *schwartzi*. Three haplotypes were identified within clade B. The average genetic distance between members of clades B and C was 5.6% (Table 2).

Clade C includes 59 specimens collected from east of the Andes Mountains in Ecuador, eastern Peru, Bolivia, Paraguay, southeastern Brazil, north and south of the Orinoco River in Venezuela, French Guiana, Trinidad, Tobago, Grenada, and Carriacou Island (Fig. 5); representing the subspecies *fallax*

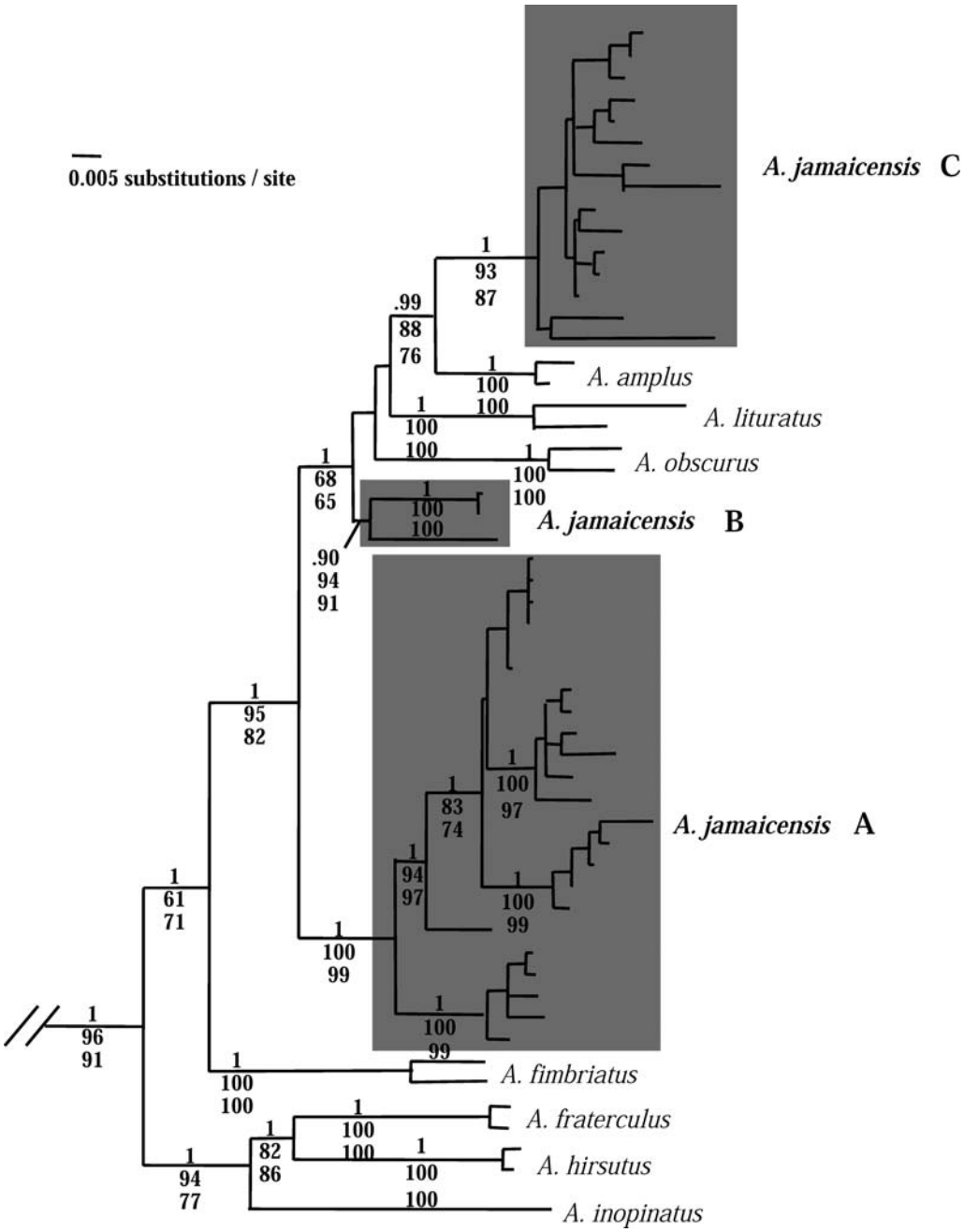

FIG. 3.—Maximum-likelihood phylogram (–lnL = 6,326.17) based on entire cytochrome-*b* sequences and the GTR+ Γ +I model of evolution. Scores are Bayesian posterior probabilities (top score) and bootstrap support values (percentage of 250 iterations) from minimum-evolution (middle score) and maximum-parsimony (bottom score) analyses. *Koopmania concolor*, *Dermanura bogotensis*, and *D. phaeotis* were used as outgroups but are not shown. Shaded regions correspond to clades A, B, and C within the *A. jamaicensis* complex (sensu Simmons 2005).

($n = 8$), *grenadensis* ($n = 6$), *hercules* ($n = 27$), *planirostris* ($n = 7$), and *trinitatis* ($n = 12$). Fifty haplotypes were identified within clade C.

DISCUSSION

Phylogenetic analysis of the cytochrome-*b* sequences from 176 individuals provides support for monophyly of all species of *Artibeus* examined (*A. inopinatus*, *A. hirsutus*, *A. fraterculus*, *A. fimbriatus*, *A. obscurus*, *A. lituratus*, and *A. amplus*; Figs. 2 and 3) except for *A. jamaicensis* (sensu Simmons 2005). *A. jamaicensis* as recognized by Simmons (2005) includes 3 distantly related (mean distance = 6%) lineages within the genus (clades A, B, and C; Figs. 2 and 3). By direct phylogenetic interpretation and to achieve monophyly for clades A, B, and C, respectively, we recognize clades A, B, and C as separate species (Phylogenetic Species Concept—sensu Mishler and Theriot 2000; see also "*Perspectives*" below). Clade A includes specimens from Jamaica, the type locality of *A. jamaicensis* (Leach 1821), therefore clade A is recognized as

TABLE 2.—Average Kimura 2-parameter distances within (in boldface, along diagonal) and among (below diagonal) *Koopmania*, *Dermanura*, species of *Artibeus*, and clades A, B, and C of *A. jamaicensis* (sensu Simmons 2005) based on entire cytochrome-*b* gene sequences. Clade A includes the traditionally recognized subspecies *aequatorialis*, *jamaicensis*, *parvipes*, *paulus*, *richardsoni*, *triomylus*, and *yucatanicus*; clade B includes *schwartzi*; and clade C includes *fallax*, *grenadensis*, *hercules*, *planirostris*, and *trinitatis*.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1) *K. concolor* ($n = 1$)	—												
2) *D. bogotensis* ($n = 1$)	0.136	—											
3) *D. phaeotis* ($n = 1$)	0.120	0.106	—										
4) *A. inopinatus* ($n = 1$)	0.112	0.131	0.124	—									
5) *A. hirsutus* ($n = 2$)	0.124	0.124	0.119	0.077	**0.005**								
6) *A. fraterculus* ($n = 2$)	0.116	0.135	0.113	0.076	0.063	**0.006**							
7) *A. fimbriatus* ($n = 2$)	0.108	0.132	0.103	0.088	0.089	0.089	**0.024**						
8) *A. obscurus* ($n = 2$)	0.101	0.138	0.116	0.082	0.092	0.089	0.077	**0.023**					
9) *A. lituratus* ($n = 2$)	0.122	0.144	0.121	0.094	0.091	0.086	0.094	0.074	**0.033**				
10) *A. amplus* ($n = 2$)	0.106	0.139	0.110	0.088	0.096	0.092	0.080	0.060	0.058	**0.008**			
11) Clade A ($n = 35$)	0.114	0.138	0.109	0.089	0.092	0.085	0.075	0.071	0.070	0.062	**0.030**		
12) Clade B ($n = 3$)	0.117	0.132	0.104	0.085	0.090	0.084	0.070	0.056	0.060	0.051	0.061	**0.025**	
13) Clade C ($n = 50$)	0.118	0.134	0.117	0.097	0.096	0.093	0.081	0.059	0.062	0.041	0.068	0.056	**0.017**

A. jamaicensis. Clade B includes specimens from St. Vincent, the type locality of *A. j. schwartzi* (Jones 1978), herein clade B is recognized as *A. schwartzi*. Finally, clade C includes specimens from Bahia, Brazil (~120 km north of Salvador), the type locality of *A. planirostris* (Spix 1823), therefore clade C is recognized as *A. planirostris*.

Recognizing *A. planirostris* and *A. schwartzi* as separate species distinct from *A. jamaicensis* is a conservative interpretation of the mitochondrial DNA results and is concordant with previous studies of systematics of *Artibeus*. First, in studies primarily directed at the zoogeographic distribution of Antillean *A. jamaicensis* (sensu lato), Pumo et al. (1988), Phillips et al. (1989), and Phillips et al. (1991) identified 3 genetic lineages (J, SV, and G) based on restriction fragment length polymorphism and restriction-site mapping of the entire mitochondrial genome. The J, SV, and G lineages correspond to our clades A, B, and C, respectively. None of the earlier studies recommended systematic changes, primarily because their experimental designs did not address species status. However, the correspondence between earlier and current studies show that our cytochrome-*b* data are representative of variation across the entire mitochondrial genome. This correspondence reduces possible concerns about pseudogene amplification or spurious ''single-gene'' results. Second, our results affirm previous morphological and molecular studies concerning the taxonomic status of *A. planirostris* (Andersen 1908; Koopman 1993; Lim 1997; Lim and Wilson 1993; Lim et al. 2004; Patten 1971). Third, recognizing *A. jamaicensis* as Simmons (2005) did would require recognizing 3 other species of *Artibeus* (*A. amplus*, *A. lituratus*, and *A. obscurus*) as conspecific members of *A. jamaicensis* (sensu lato). Data from several sources make this interpretation undesirable and complicated, because morphological and ecological data document the sympatric distributions of *A. lituratus*, *A. obscurus*, and *A. amplus* with *A. jamaicensis* (sensu Simmons 2005; Handley 1987, 1989; Haynes and Lee 2004; Lim and Wilson 1993; Marques-Aguiar 1994; Patten 1971). Herein, *A. jamaicensis* and *A. schwartzi* are documented sympatrically in the northern Lesser Antilles (Nevis, St. Kitts, and Monsterrat). Additionally, *A. jamaicensis*, *A. planirostris*, and *A. schwartzi* are sympatric in the southern Lesser Antilles on Grenada, Carriacou, St. Vincent, St. Lucia, and Barbados. Sympatric occurrence of mitochondrial haplotypes does not exclude the possibility of hybridization.

TABLE 3.—Average Kimura 2-parameter distances within (in boldface, along diagonal) and among (below diagonal) subspecies of *Artibeus jamaicensis* (sensu Simmons 2005) based on entire cytochrome-*b* gene sequences.

	1	2	3	4	5	6	7	8	9	10	11	12	13
1) *aequatorialis* ($n = 11$)	**0.008**												
2) *fallax* ($n = 8$)	0.068	**0.019**											
3) *grenadensis* ($n = 6$)	0.066	0.017	**0.001**										
4) *hercules* ($n = 27$)	0.067	0.018	0.019	**0.014**									
5) *jamaicensis* ($n = 57$)	0.044	0.065	0.061	0.065	**0.000**								
6) *parvipes* ($n = 1$)	0.044	0.064	0.060	0.064	0.001	—							
7) *paulus* ($n = 3$)	0.045	0.074	0.069	0.075	0.021	0.022	**0.007**						
8) *planirostris* ($n = 7$)	0.069	0.019	0.019	0.018	0.066	0.065	0.075	**0.017**					
9) *richardsoni* ($n = 6$)	0.045	0.070	0.066	0.071	0.023	0.023	0.012	0.071	**0.017**				
10) *schwartzi* ($n = 13$)	0.058	0.056	0.057	0.054	0.057	0.056	0.066	0.057	0.064	**0.006**			
11) *trinitatis* ($n = 18$)	0.067	0.018	0.006	0.020	0.062	0.061	0.070	0.018	0.067	0.057	**0.007**		
12) *triomylus* ($n = 5$)	0.048	0.069	0.066	0.068	0.026	0.026	0.032	0.071	0.034	0.059	0.066	**0.010**	
13) *yucatanicus* ($n = 5$)	0.042	0.067	0.064	0.067	0.007	0.007	0.018	0.068	0.021	0.059	0.064	0.026	**0.011**

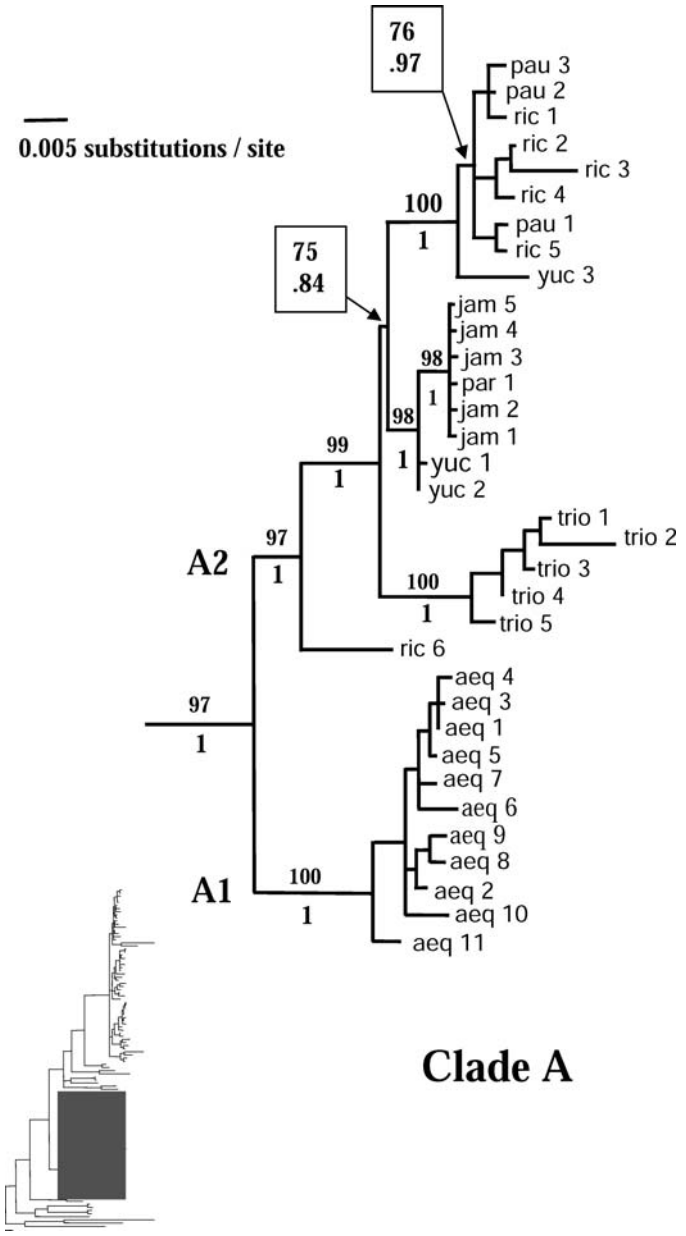

FIG. 4.—Clade A from Fig. 2. Scores above and below branches are bootstrap support values (maximum parsimony) and Bayesian posterior probabilities, respectively. Haplotypes are coded by subspecies: aeq = *aequatorialis*, jam = *jamaicensis*, pau = *paulus*, ric = *richardsoni*, trio = *triomylus*, and yuc = *yucatanicus*. See Fig. 1 for subspecies distributions and Appendix I for detailed haplotype information. A1 and A2 represent clades containing *aequatorialis* and the Central American, Mexican, and Caribbean subspecies, respectively.

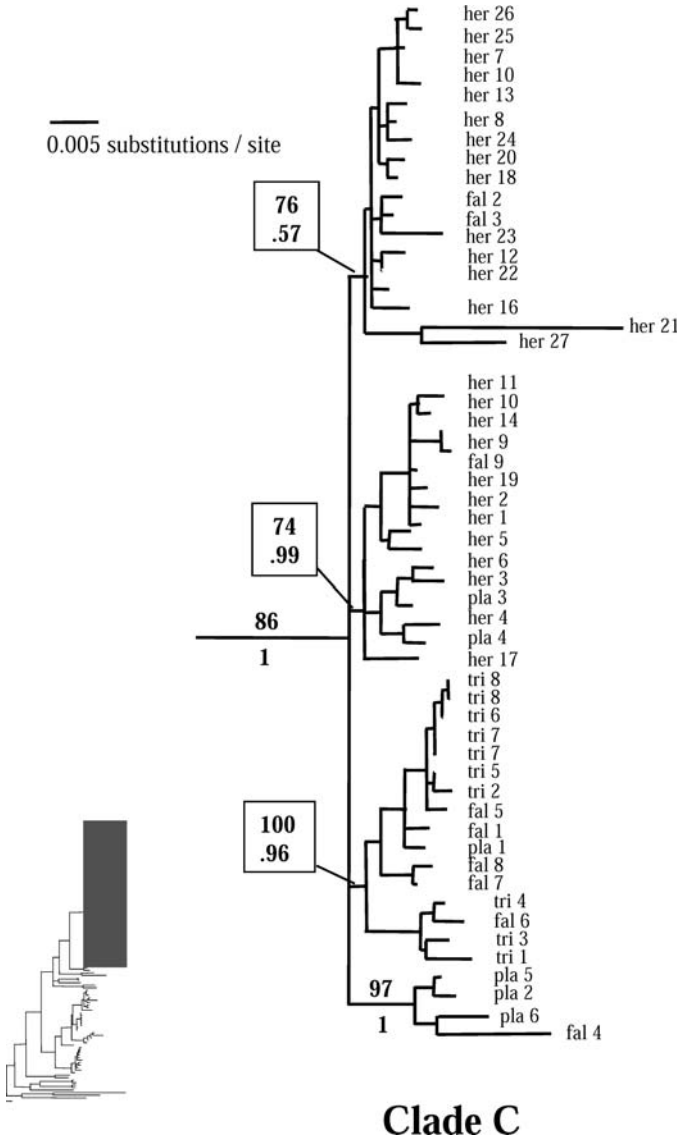

FIG. 5.—Clade C from Fig. 2. Scores above and below branches are bootstrap support values (maximum parsimony) and Bayesian posterior probabilities, respectively. Haplotypes are coded by subspecies: her = *hercules*, fal = *fallax*, pla = *planirostris*, and tri = *trinitatis*. See Fig. 1 for subspecies distributions and Appendix I for detailed haplotype information. C1 represents the clade containing *trinitatis*, *grenadensis*, and 4 specimens of *fallax* collected from French Guiana and Venezuela.

Distribution of A. jamaicensis and A. planirostris.—The distribution of *A. jamaicensis* has varied in the literature according to taxonomy (Table 1). Some authors have described this species as occurring from northern Argentina, throughout South America, the Caribbean, Central America, and Mexico (Hershkovitz 1949; Marques-Aguiar 1994; Ortega and Castro-Arellano 2001). Others have assigned a more limited distribution (Koopman 1993; Lim 1997; Patten 1971). These differences in geographic range are primarily the function of the taxonomic status of *planirostris*, with some authors recognizing this form as a separate species and others considering it as a subspecies of *A. jamaicensis* (Table 1).

Based on the mitochondrial DNA data herein and in Phillips et al. (1989, 1991) and Pumo et al. (1996), the distribution of *A. jamaicensis* (a statistically supported monophyletic group; clade A) is much more restricted than traditionally thought, from west of the Andes Mountains in South America, northward throughout Central America and southern Mexico, eastward throughout the Greater Antilles, and southward to Grenada (Figs. 6a and 6b). Furthermore, the distribution of

A. planirostris (a statistically supported monophyletic group; clade C) is more widespread than previously thought (Andersen 1908; Hollis 2005; Koopman 1993; Lim 1997; Patten 1971). The range actually includes the area north of the Orinoco River and Llanos Savannah in Venezuela and in the southern Lesser Antilles it is found as far north as St. Lucia (Phillips et al. 1989, 1991; Pumo et al. 1988, 1996; Figs. 6a and 6b).

Lim (1997), based on morphometric analysis of a large sample ($n = 351$) of specimens collected throughout Venezuela and northwestern Guyana, hypothesized that *A. jamaicensis* and *A. planirostris* occur roughly north and south, respectively, of the Orinoco River, corresponding to a difference in body size: small-bodied *A. jamaicensis* north of the Orinoco River and large-bodied *A. planirostris* south of the Orinoco River. However, our samples of the small-bodied specimens (R. Marchán, pers. comm.) collected from north of the Orinoco River in Venezuela, and from Trinidad, Tobago, and Grenada, all are identified by mitochondrial cytochrome-*b* sequences as *A. planirostris* (clade C). Thus, the presence of individuals with haplotypes of *A. jamaicensis* (clade A) remain to be documented north of the Orinoco River in Venezuela. Based on examination of our cytochrome-*b* data it is hypothesized that the morphological variation reported by Lim (1997) represents intraspecific variation within *A. planirostris*, resulting from ecogeographic effects on body size. Smaller individuals of *A. planirostris* probably occur in the drier regions of the Llanos Savannah north of the Orinoco River, and larger individuals in the more tropical and humid regions south of the Llanos Savannah and Orinoco River. Similar correlations between body size and moist versus xeric regions has been documented for vespertilionid bats (*Eptesicus fuscus*—Burnett 1983) and even noted within the genus *Artibeus* (Davis 1970, 1984; Marques-Aguiar 1994). Further investigation is required to explain the morphological variation reported by Lim (1997) and to test the hypothesis of an ecogeographic effect on body size.

Origin of A. jamaicensis.—Within our data, the origin of the ancestral population of *A. jamaicensis* is unclear. Examination of the cytochrome-*b* data suggests either a Central American or western South American origin for *A. jamaicensis* (clade A). The basal clades within *A. jamaicensis* (A1 and A2; Fig. 4) give rise to *A. j. aequatorialis* in western Ecuador (A1) and to populations in Central America and the Caribbean (A2). Our sample from western Ecuador suggests a fairly recent common ancestor for populations referable to *A. j. aequatorialis*, after an extensive period of isolation from the Central American and Caribbean populations. The observation that *A. j. aequatorialis* and the basal branch of clade A2 is from Panama suggests a Panamanian or west of the Andes basal stock that then gave rise to Central American, Mexican, and Caribbean populations. The southeastern Mexican and Caribbean haplotypes are most derived in a rooted tree and populations of *A. jamaicensis* distributed throughout the Greater and Lesser Antilles (Fig. 4; Appendix I) are characterized by a lack of genetic diversity (Kimura 2-parameter distance = 0%). Given that haplotypes from the Yucatan Peninsula are the same as those from the Caribbean, *A. jamaicensis* likely invaded the Caribbean across the Yucatan Channel into Cuba and Jamaica. Given the absence of genetic diversity this probably occurred during periods of low sea levels late in the Pleistocene (Genoways et al. 2005; Phillips et al. 1991). The occurrence of related haplotypes in Yucatan implies that the mainland was the source of the insular invasion rather than the Caribbean populations being the source of Central American populations (Fig. 4; Appendix I).

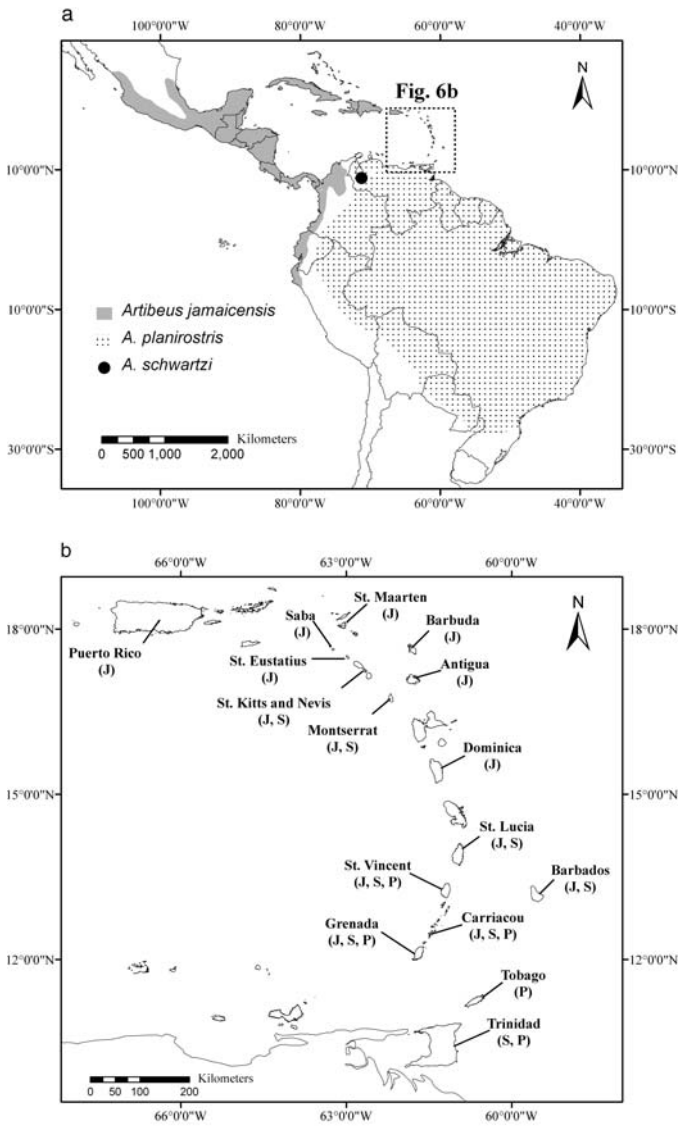

FIG. 6.—Distributions *of Artibeus jamaicensis*, *A. planirostris*, and *A. schwartzi* based on phylogenetic analysis of cytochrome-*b* DNA sequences. a) Mexican, Central American, Caribbean, and South American distributions. b) Lesser Antillean distribution of *A. jamaicensis* (J), *A. planirostris* (P), and *A. schwartzi* (S) according to the data reported herein and from Phillips et al. (1989, 1991) and Pumo et al. (1988, 1996).

Geographic variation.—Samples collected from within the ranges of all putative subspecies of *A. jamaicensis* (sensu Simmons 2005) were included in the current analysis. Our results indicate that the genetic basis and geographic limits of

several subspecies could require revision. We recommend further studies using both morphological and genetic data to create a comprehensive description of geographic and subspecific variation within *A. jamaicensis* and *A. planirostris*. Such data will provide a chance to test the correlation of geographic variation in morphology with patterns in genetic divergence. Nonetheless, our results from mitochondrial DNA show the presence of geographic structuring within *A. jamaicensis* (clade A) and the absence of geographic structuring within *A. planirostris* (clade C).

Subspecies in A. jamaicensis (clade A).—Lineage A1 (Fig. 4) of *A. jamaicensis* is composed entirely of specimens collected from within the range, including the type locality of the subspecies *aequatorialis* (Zaruma, Ecuador—Andersen 1906). Members of *aequatorialis* form a well-supported clade sister to the Central American, Mexican, and Caribbean subspecies and have a greater genetic distance (4.4%) from *A. j. jamaicensis* than does any other subspecies in clade A. Given the phylogenetic placement and genetic distance, and a lack of information from other data sources (e.g. morphology, ecology, and nuclear DNA), we provisionally retain *aequatorialis* as a subspecies of *A. jamaicensis*. However, new detailed studies of *aequatorialis* are clearly warranted, especially considering its genetic distance and monophyly relative to lineage A2 (Fig. 4; Baker and Bradley 2006).

Lineage A2 of *A. jamaicensis* includes specimens collected from within the ranges of the subspecies *jamaicensis*, *parvipes*, *paulus*, *richardsoni*, *triomylus*, and *yucatanicus*. Guerrero et al. (2004) used morphometric data, reciprocal monophyly of cytochrome-*b* data, and the Phylogenetic Species Concept (sensu Mishler and Theriot 2000) to elevate *triomylus* to specific status. Their results appear to be extremely sensitive to, or dependent upon, taxon sampling. Based on our cytochrome-*b* data, recognizing *A. triomylus* as a separate species results in further paraphyly of members of clade A (Fig. 4). In the current analysis 2.6% mean genetic distance separates *triomylus* from *jamaicensis*, whereas the other Central American and Mexican subspecies average 2.0% divergence from *jamaicensis*. Therefore, pending further study, *triomylus* is returned to subspecific status (sensu Handley 1966). The genetic subdivisions (Fig. 4) are inconsistent with most of the remaining named subspecies within lineage A2. This will necessitate a review of the morphological and genetic variation among populations of *A. jamaicensis* throughout Central America, Mexico, and the Caribbean. The exception is *A. j. jamaicensis*, which occurs from the Greater Antilles to the Lesser Antilles.

Subspecies in A. planirostris (clade C).—The phylogeographic patterns within *A. planirostris* (Fig. 5) are not as structured as those within *A. jamaicensis* (Fig. 4). However, the clade containing samples of subspecies *trinitatis* and *grenadensis* (C1; Fig. 5) is well supported and provides evidence for an invasion of *A. planirostris* from northern Venezuela and the Guiana Shield into the southern Lesser Antilles. Much like *A. jamaicensis*, Antillean populations of *A. planirostris* are characterized by low sequence diversity (Fig. 5; Appendix I). The lack of defined geographic structuring for the remainder of the samples of *A. planirostris* is significant in as much as this includes members of the named subspecies *planirostris*, *fallax*, and *hercules* (Koopman 1978; see Hollis 2005). Lim et al. (2004) observed a similar lack of geographic structuring in their samples of *A. planirostris* from Venezuela and the Guiana Shield and hypothesized events of rapid radiation within the genus. We agree that a rapid radiation and dispersal could account for the present distribution of, and variation within, populations of *A. planirostris* distributed throughout northern South America and into the Caribbean.

Taxonomic status and distribution of A. schwartzi.—Jones (1978), noting the large size of specimens collected from the island of St. Vincent, described and named *A. j. schwartzi* for this insular population of *Artibeus*. Pumo et al. (1988) subsequently identified the genetic distinctiveness of *A. j. schwartzi* as compared to *A. j. jamaicensis* and hypothesized that the 2 subspecies diverged nearly 4 million years ago. Additionally, Carstens et al. (2004), based on a smaller sample of cytochrome-*b* data, identified a distinct lineage within populations of *A. jamaicensis* from Nevis, St. Kitts, and Montserrat. We now know that these specimens have haplotypes identifiable as *schwartzi*. Carstens et al. (2004) also tested for and rejected incomplete lineage sorting as an explanation for the genetic diversity observed within their sample of *A. jamaicensis* (which included *schwartzi*). From both anagenic (Evolutionary Species Concept—sensu Wiley 1978) and cladogenic perspectives (Phylogenetic Species Concept—sensu Mishler and Theriot 2000) of the cytochrome-*b* results, *schwartzi* should be recognized as a species distinct from *A. jamaicensis* and *A. planirostris* (clade B; Fig. 2). Furthermore, the observation that *A. schwartzi* attained a distinct morphology (Jones 1978) and reciprocal monophyly of the mitochondrial genome is compatible with specific status as defined by the Genetic Species Concept (Baker and Bradley 2006).

Based on our analysis, the distribution of *A. schwartzi* (clade B) is geographically limited. Relatively few specimens from outside of the southern Lesser Antilles have been identified as having the haplotype and phenotype of *A. schwartzi*. Thus far, specimens with the haplotype of *A. schwartzi* have been collected from Barbados, Bequia, Grenada, St. Lucia, and St. Vincent (Phillips et al. 1989; Pumo et al. 1988, 1996) and from Carriacou, Nevis, Montserrat, St. Kitts, and south of Lake Maracaibo in Venezuela (Figs. 6a and 6b).

Origin of A. schwartzi.—Three previous hypotheses have been given for the origin of *A. schwartzi*, although each was formulated in the context of recognizing *schwartzi* as a subspecies rather than as a species. First, Jones (1989) hypothesized that the morphologically distinct population of *A. schwartzi* on St. Vincent was an example of heterosis, originating by hybridization between subspecies of *A. jamaicensis* from north and south of St. Vincent. The mitochondrial haplotype of *A. schwartzi* from St. Vincent is as distinct from Caribbean populations of *A. jamaicensis* (5.7%) as it is from Caribbean populations of *A. planirostris* (5.6%). It is highly improbable that the haplotype of *A. schwartzi* is a result of hybridization given that mitochondrial DNA is a maternally inherited, nonrecombining, haploid genome (Moritz et al.

1987; Nishimura et al. 2006). Recombination of the vertebrate mitochondrial genome would require cleavage and subsequent recombination of existing sequences. It is doubtful that this would occur in the cytochrome-*b* gene. However, see Ladoukakis and Zouros (2001a, 2001b), Rokas et al. (2003), and Smith and Smith (2002) for recent evidence of animal mitochondrial DNA recombination.

Second, Phillips et al. (1989) hypothesized that *A. schwartzi* once occurred throughout the Caribbean and subsequent to the invasion by *A. jamaicensis* (from Mexico and Central and South America) it became extinct, or genetically swamped, on all of the islands except for St. Vincent. Phillips et al. (1989) extended this hypothesis further, suggesting that *schwartzi* represented a relictual population of the supposedly extinct *A. anthonyi* from Cuba. This can be tested by extracting DNA and generating cytochrome-*b* sequence data from subfossil material on Cuba, the type locality of *A. anthonyi* (Woloszyn and Silva-Taboada 1977). If the DNA sequence from the subfossils is sufficiently similar to *A. schwartzi* then *A. anthonyi* would be the senior synonym for the specimens recognized as *A. schwartzi* in this study.

Finally, Pumo et al. (1996) hypothesized both a South American origin for *A. schwartzi* and a close relationship with *A. planirostris*. This hypothesis was based on morphological comparisons with northern South American *Artibeus* (Lim and Wilson 1993) in conjunction with sequence data from the 12S ribosomal RNA gene. However, the specimens of *A. planirostris* and *A. jamaicensis* as defined by Lim and Wilson (1993) were collected from within the ranges of the subspecies *fallax* (large-bodied) and *trinitatis* (small-bodied; herein *A. p. trinitatis*), respectively. Therefore, the large phenotype of *schwartzi* was most similar to the phenotype of *A. p. fallax* and it remains to be documented whether or not *A. jamaicensis* was sampled by Lim and Wilson (1993). Examination of cytochrome-*b* data does not support the close genetic relationship between *A. schwartzi* and *A. planirostris* (Table 2; Fig. 2). Additionally, we generated cytochrome-*b* DNA sequence data from the same specimen of *A. planirostris* (CMNH 83901) used by Pumo et al. (1996) for comparison of 12S ribosomal RNA sequence data with that of *schwartzi*. Our results confirmed that this specimen was appropriately identified as *A. planirostris*.

Examination of our data indicates that *A. schwartzi* likely invaded the Caribbean from northern South America, a hypothesis supported by the sister haplotype from a single specimen collected from south of Lake Maracaibo in Venezuela (Fig. 6a). The alternative, a Caribbean origin, does not explain the lack of variability in the cytochrome-*b* gene for the Caribbean specimens of *A. schwartzi*. Our southernmost and northernmost Antillean specimens of *A. schwartzi*, from Grenada and St. Kitts, respectively, are genetically identical yet are geographically separated by at least 600 km. This lack of variability, similar to the Caribbean populations of *A. jamaicensis* and *A. planirostris*, suggests that the occurrence of *A. schwartzi* in the Caribbean resulted from recent invasion or expansion events. However, from morphological examinations (measurements taken in the field and 1 available skull), specimens collected from places other than St. Vincent are unlike the St. Vincent populations of *A. schwartzi*, and actually are morphologically similar to *A. jamaicensis* ($n = 3$) or *A. planirostris* ($n = 1$). Could there be introgression of the haplotype of *A. schwartzi* into populations of *A. jamaicensis* in the northern Antilles and similar introgression into *A. planirostris* to the south? Alternatively, could these similar phenotypes be explained by ecomorphological convergence? Morphological and nuclear DNA analyses would be required to adequately test the hypotheses of introgression and ecomorphological convergence.

Perspectives.—Using cytochrome-*b* DNA sequence criteria, populations with haplotypes of *A. jamaicensis* remain to be documented in South America east of the Andes Mountains. Additionally, using the same criteria, *Artibeus jamaicensis*, *A. planirostris*, and *A. schwartzi* are sympatric in the Caribbean but it is likely that they hybridize, especially in light of the morphological data in Genoways et al. (1998). The possibility of hybridization in combination with a choice of species concept (Biological—Mayr 1942; Phylogenetic—Mishler and Theriot 2000; Genetic—Baker and Bradley 2006) will ultimately result in the recognition of alternative numbers of species within *A. jamaicensis* (sensu Simmons 2005).

The mitochondrial DNA data presented herein document the presence of individuals with the cytochrome-*b* sequences of *A. jamaicensis*, *A. planirostris*, and *A. schwartzi* on the small island of Carriacou in the southern Lesser Antilles. It is improbable that 3 species of *Artibeus* can coexist over time on this small, xeric, and ecologically monotypic island. The morphological variation of these specimens observed in the field suggested that only a single species of *Artibeus* was present (HHG and RJB). If external phenotype or traditional cranial and dental morphology are used as the criterion for recognizing species, then the most logical explanation for 3 cytochrome-*b* haplotypes being present in a small island population is that hybridization has resulted in survival of 3 relatively ancient mitochondrial lineages within a single population. Meanwhile, presumably the nuclear genome has recombined in some subset of the nuclear genes present in the 3 maternal lineages, resulting in a phenotype typical of Caribbean specimens of *A. jamaicensis* (clade A). Whatever the case might be, an understanding of the biology of *Artibeus* on small Caribbean islands will require further research.

If the hybridization and nuclear genome swamping of 3 maternal lineages is true, what are the implications? Is hybridization and swamping a unique characteristic of island ecology, or would these ''species'' hybridize at any location where they come into contact? It is clear that *A. lituratus* and *A. obscurus* have evolved mechanisms that allow them to be genetically isolated from each other as well as permitting sympatry with *A. jamaicensis* and *A. planirostris* without hybridization. Although using genetic distances to predict the completion of speciation and development of genetic isolating mechanisms is predicted to have a failure rate (Baker and Bradley 2006), the magnitude of genetic divergence separating *A. jamaicensis*, *A. planirostris*, and *A. schwartzi* essentially equals the magnitude of genetic divergence distinguishing

A. lituratus, *A. obscurus*, and *A. jamaicensis* (Table 2). The significance of this observation is that clades of organisms with similar reproductive cycles, gestation periods, feeding strategies, and body sizes can be highly variable in the time required to evolve genetic or reproductive isolation. Such differential rates of genetic isolation would occur if the Bateson–Dobzhansky–Muller model was the mechanism by which genetic isolation is evolving (Baker and Bradley 2006).

Resumen

La filogenética y filogeografía del murciélago frutero de Jamaica (*Artibeus jamaicensis*) fueron examinadas en base a análisis de variación de secuencias del ADN en el gen mitocondrial citocromo-*b* de 176 muestras representando todas las 13 subespecies de *A. jamaicensis* (sensu Simmons 2005). Los resultados muestran que *A. jamaicensis* (sensu Simmons 2005) comprende 3 grupos monofiléticos los cuales están separados filogenéticamente por la presencia de *A. obscurus*, *A. lituratus*, y *A. amplus*. Según la variación de la secuencia del ADN mitocondrial, *A. jamaicensis*, *A. schwartzi*, y *A. planirostris* son los nombres específicos adecuados para estos linajes. Haplotipos identificables como *A. jamaicensis* fueron ausentes al este de los Andes en Sudamérica, haplotipos de *A. schwartzi* fueron documentados a través de las Antillas menores y del norte de Venezuela, y haplotipos de *A. planirostris* fueron identificados al este de los Andes en Sudamérica, al norte del Río Orinoco en Venezuela, y en las Antillas menores del sur. Haplotipos de *Artibeus jamaicensis*, *A. schwartzi*, y *A. planirostris* fueron simpatricamente en Carriacou, una pequeña isla en las Antillas menores del sur que es ecológicamente monotípica. La magnitud de divergencia genética separando *A. jamaicensis*, *A. planirostris*, y *A. schwartzi* es esencialmente igual a la magnitud de divergencia genética que distingue a *A. lituratus*, *A. obscurus*, y *A. jamaicensis*. Estudios del genoma nuclear serán necesarios para entender las implicancias biológicas de estos patrones en el genoma mitocondrial.

Acknowledgments

The substance of this manuscript was submitted by PAL to the Department of Biology of Texas Tech University, Lubbock, in partial fulfillment of the Master of Science in Biology degree. We thank R. Marchán and S. Burneo of the Museo de Zoologia of the Pontificia Universidad Catolica del Ecuador for loans of tissue material. We also thank B. C. Carstens for loaning tissue material. We are grateful to H. J. Garner, K. McDonald, J. P. Carrera, and J. B. Chavez of the Natural Science Research Laboratory of the Museum of Texas Tech University for assistance with loans of tissue material. S. Solari provided insightful comments and suggestions that helped improve this manuscript. H. Mantilla-Meluk assisted with generating distribution maps. This study would not have been possible were it not for the collecting efforts of R. D. Bradley, C. Jones, G. G. Kwiecinski, R. D. Owen, M. R. Willig, T. E. Lee, Jr., R. Stevens, and members of the Sowell 2001 and 2004 expeditions. Financial support was provided by J. Sowell, A. Brown, and the Texas Tech University Biological Database Program.

Literature Cited

Andersen, K. 1906. Brief diagnoses of a new genus and ten new forms of stenodermatous bats. Annals and Magazine of Natural History, Series 7, 18:419–423.

Andersen, K. 1908. A monograph of the chiropteran genera *Uroderma*, *Enchisthenes*, and *Artibeus*. Proceedings of the Zoological Society of London 1908:204–319.

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Baker, R. J., and R. D. Bradley. 2006. Speciation in mammals and the Genetic Species Concept. Journal of Mammalogy 87:643–662.

Baker, R. J., S. R. Hoofer, C. A. Porter, and R. A. Van Den Bussche. 2003. Diversification among New World leaf nosed bats: an evolutionary hypothesis and classification inferred from digenomic congruence of DNA sequence. Occasional Papers, Museum of Texas Tech University 230:1–32.

Bradley, R. D., and R. J. Baker. 2001. A test of the Genetic Species Concept: cytochrome-*b* sequences and mammals. Journal of Mammalogy 82:960–973.

Burnett, C. D. 1983. Geographic and climatic correlates of morphological variation in *Eptesicus fuscus*. Journal of Mammalogy 64:437–444.

Carstens, B. C., J. Sullivan, L. M. Davalos, P. A. Larsen, and S. C. Pedersen. 2004. Exploring population and genetic structure in three species of Lesser Antillean bats. Molecular Ecology 13:2557–2566.

Davalos, L. M., and S. A. Jansa. 2004. Phylogeny of the Lonchophyllini (Chiroptera: Phyllostomidae). Journal of Mammalogy 85:404–413.

Davis, W. B. 1970. The large fruit bats (genus *Artibeus*) of Middle America, with a review of the *Artibeus jamaicensis* complex. Journal of Mammalogy 51:105–122.

Davis, W. B. 1984. Review of the large fruit-eating bats of the *Artibeus* ''*lituratus*'' complex (Chiroptera: Phyllostomidae) in Middle America. Occasional Papers, Museum of Texas Tech University 93:1–16.

Eisenberg, J. F. 1989. Mammals of the Neotropics, the northern Neotropics. University of Chicago Press, Chicago, Illinois.

Fleming, T. H. 1971. *Artibeus jamaicensis*: delayed embryonic development in a neotropical bat. Science 171:401–404.

Genoways, H. H., R. J. Baker, J. W. Bickham, and C. J. Phillips. 2005. Bats of Jamaica. Special Publications, The Museum, Texas Tech University 48:1–155.

Genoways, H. H., C. J. Phillips, and R. J. Baker. 1998. Bats of the Antillean island of Grenada: a new zoogeographic perspective. Occasional Papers, The Museum, Texas Tech University 177: 1–28.

Guerrero, J. A., E. D. Luna, and D. Gonzalez. 2004. Taxonomic status of *Artibeus jamaicensis triomylus* inferred from molecular and morphometric data. Journal of Mammalogy 85:866–874.

Hall, E. R. 1981. The mammals of North America. 2nd edition. John Wiley & Sons, Inc., New York.

Handley, C. O., Jr. 1966. Descriptons of new bats (*Chiroderma* and *Artibeus*) from Mexico. Anales del Instituto de Biologia, University of Mexico 36:297–301.

Handley, C. O., Jr. 1987. New species of mammals from northern South America: fruit-eating bats, genus *Artibeus* Leach. Pp. 163–172 in Studies in neotropical mammalogy, essays in honor of Phillip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana: Zoology (New Series) 39:1–506.

HANDLEY, C. O., JR. 1989. The *Artibeus* of Gray, 1838. Pp. 443–468 in Advances in neotropical mammalogy (K. H. Redford and J. F. Eisenburg, eds.). Sandhill Crane Press, Gainsville, Florida.

HANDLEY, C. O., JR., A. L. GARDNER, AND D. E. WILSON. 1991a. Movements. Pp. 89–130 in Demography and natural history of the common fruit bat *Artibeus jamaicensis* on Barro Colorado Island, Panama (C. O. Handley, Jr., D. R. Wilson, and A. L. Gardner, eds.). Smithsonian Institution Press, Washington, D.C.

HANDLEY, C. O., JR., A. L. GARDNER, AND D. E. WILSON. 1991b. Food habits. Pp. 141–146 in Demography and natural history of the common fruit bat *Artibeus jamaicensis* on Barro Colorado Island, Panama (C. O. Handley, Jr., D. R. Wilson, and A. L. Gardner, eds.). Smithsonian Institution Press, Washington, D.C.

HAYNES, M. A., AND T. E. LEE, JR. 2004. *Artibeus obscurus*. Mammalian Species 752:1–5.

HERSHKOVITZ, P. 1949. Mammals of northern Colombia. Preliminary reports no. 5: bats (Chiroptera). Proceedings of the United States National Museum 99:429–454.

HOFFMANN, F. G., AND R. J. BAKER. 2001. Systematics of bats of the genus *Glosssophaga* (Chiroptera: Phyllostomidae) and phylogeography of *G. soricina* based on the cytochrome-*b* gene. Journal of Mammalogy 82:1092–1101.

HOLLIS, L. 2005. *Artibeus planirostris*. Mammalian Species 775:1–6.

HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL (EDS.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas.

HUELSENBECK, J. P., AND F. RONQUIST. 2001. MrBayes: Bayesian inference of phylogeny. Bioinformatics 17:745–755.

JONES, J. K., JR. 1978. A new bat of the genus *Artibeus* from the Lesser Antillean island of St. Vincent. Occasional Papers, The Museum, Texas Tech University 51:1–6.

JONES, J. K., JR. 1989. Distribution and systematics of bats in the Lesser Antilles. Pp. 645–659 in Biogeography of the West Indies: past, present, and future (C. A. Woods, ed.). Sandhill Crane Press, Gainsville, Florida.

JONES, J. K., JR., AND D. C. CARTER. 1976. Annotated checklist, with keys to subfamilies and genera. Pp. 7–38 in Biology of the bats of the New World family Phyllostomatidae. Part I (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.). Special Publications, The Museum, Texas Tech University Press 10:1–218.

JONES, J. K., JR., AND C. J. PHILLIPS. 1970. Comments on systematics and zoogeography of bats in the Lesser Antilles. Studies on the Fauana of Curacao and Other Caribbean Islands 32:131–145.

KOOPMAN, K. F. 1968. Taxonomic and distributional notes on Lesser Antillean bats. American Museum Novitates 2333:1–13.

KOOPMAN, K. F. 1978. Zoogeography of Peruvian bats, with special emphasis on the role of the Andes. American Museum Novitates 2651:1–33.

KOOPMAN, K. F. 1982. Biogeography of the bats of South America. Pp. 273–302 in Mammalian biology in South America (M. A. Mares and H. H. Genoways, eds.). Special Publications of the Pymatuning Lab 6, University of Pittsburgh, Pittsburgh, Pennsylvania.

KOOPMAN, K. F. 1993. Order Chiroptera. Pp. 137–242 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). 2nd ed. Smithsonian Institution Press, Washington, D.C.

KOOPMAN, K. F. 1994. Chiroptera: systematics. Handbook of zoology. Vol. VIII: Mammalia (J. Niethammer, H. Schliemann, and D. Starck, eds.). Walter de Gruyter, Berlin, Germany 60:1–217.

KUMAR, S., K. TAMURA, AND M. NEI. 2004. MEGA 3: integrated software for molecular evolutionary genetics analysis and sequence alignment. Briefings in Bioinformatics 5:150–163.

LADOUKAKIS, E. D., AND E. ZOUROS. 2001a. Direct evidence for homologous recombination in mussel (*Mytilus galloprovincialis*) mitochondrial DNA. Molecular Biology and Evolution 18:1168–1175.

LADOUKAKIS, E. D., AND E. ZOUROS. 2001b. Recombination in animal mitochondrial DNA: evidence from published sequences. Molecular Biology and Evolution 18:2127–2131.

LEACH, W. E. 1821. The characters of seven genera of bats with foliaceous appendages to the nose. Transactions of the Linnean Society of London 13:73–82.

LIM, B. K. 1997. Morphometric differentiation and species status of the allopatric fruit-eating bats *Artibeus jamaicensis* and *A. planirostris* in Venezuela. Studies on Neotropical Fauna and Environment 32:65–71.

LIM, B. K., M. D. ENGSTROM, T. E. LEE, J. C. PATTON, AND J. W. BICKHAM. 2004. Molecular differentiation of large species of fruit-eating bats (*Artibeus*) and phylogenetic relationships based on the cytochrome *b* gene. Acta Chiropterologica 6:1–12.

LIM, B. K., AND D. E. WILSON. 1993. Taxonomic status of *Artibeus amplus* (Chiroptera: Phyllostomidae) in northern South America. Journal of Mammalogy 74:763–768.

LONGMIRE, J. L., M. MALTBIE, AND R. J. BAKER. 1997. Use of ''lysis buffer'' in DNA isolation and its implication for museum collections. Occasional Papers, The Museum, Texas Tech University 163:1–3.

MADDISON, D. R., AND W. R. MADDISON. 2000. MacClade 4. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

MARQUES-AGUIAR, S. A. 1994. A systematic review of the large species of *Artibeus* Leach, 1821 (Mammalia: Chiroptera), with some phylogenetic inferences. Boletim do Museu Paraense Emilio Goeldi, Zoologia 10:3–83.

MAYR, E. 1942. Systematics and the origin of species. Columbia University Press, New York.

MISHLER, B. D., AND E. THERIOT. 2000. The Phylogenetic Species Concept (sensu Mishler and Theriot): monophyly, apomorphy, and Phylogenetic Species Concepts. Pp. 44–54 in Species concepts and phylogenetic theory (Q. D. Wheeler and R. Meier, eds.). Columbia University Press, New York.

MORITZ, C., T. E. DOWLING, AND W. M. BROWN. 1987. Evolution of animal mitochondrial DNA: relevance for population biology and systematics. Annual Review of Ecology and Systematics 18:269–292.

NISHIMURA, Y., ET AL. 2006. Active digestion of sperm mitochondrial DNA in single living sperm revealed by optical tweezers. Proceedings of the National Academy of Sciences 103:1382–1387.

ORTEGA, J., AND H. T. ARITA. 1999. Structure and social dynamics of harem groups of *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Journal of Mammalogy 80:1173–1185.

ORTEGA, J., AND I. CASTRO-ARELLANO. 2001. *Artibeus jamaicensis*. Mammalian Species 662:1–12.

OWEN, R. D. 1987. Phylogenetic analyses of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). Special Publications, The Museum, Texas Tech University 26:1–65.

PATTEN, D. R. 1971. A review of the large species of *Artibeus* (Chiroptera: Phyllostomatidae) from western South America. Ph.D. dissertation, Texas A&M University, College Station.

PHILLIPS, C. J., D. E. PUMO, H. H. GENOWAYS, AND P. E. RAY. 1989. Caribbean island zoogeography: a new approach using mitochondrial DNA to study neotropical bats. Pp. 661–684 in Biogeography

of the West Indies (C. A. Woods, ed.). Sandhill Crane Press, Gainesville, Florida.

PHILLIPS, C. J., D. E. PUMO, H. H. GENOWAYS, P. E. RAY, AND C. A. BRISKEY. 1991. Mitochondrial DNA evolution and phylogeography in two neotropical fruit bats, *Artibeus jamaicensis* and *Artibeus lituratus*. Pp. 97–123 in Latin American mammalogy: history, biodiversity, and conservation (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman.

POSADA, D. 2004. Collapse 1.2. Brigham Young University, Provo, Utah.

POSADA, D., AND K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. Bioinformatics 14:817–818.

PUMO, D. E., E. Z. GOLDIN, B. ELLIOT, C. J. PHILLIPS, AND H. H. GENOWAYS. 1988. Mitochondrial DNA polymorphism in three Antillean island populations of the fruit bat, *Artibeus jamaicensis*. Molecular Biology and Evolution 5:79–89.

PUMO, D. E., P. S. FINAMORE, W. R. FRANEK, C. J. PHILLIPS, S. TARZAMI, AND D. BALZARANO. 1998. Complete mitochondrial genome of a neotropical fruit bat, *Artibeus jamaicensis*, and a new hypothesis of the relationships of bats to other eutherian mammals. Journal of Molecular Evolution 47:709–717.

PUMO, D. E., K. I. REMSEN, C. J. PHILLIPS, AND H. H. GENOWAYS. 1996. Molecular systematics of the fruit bat, *Artibeus jamaicensis*: origin of an unusual island population. Journal of Mammalogy 77:491–503.

REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics. University of Chicago Press, Chicago, Illinois.

ROKAS, A., E. LADOUKAKIS, AND E. ZOUROS. 2003. Animal mitochondrial DNA recombination revisited. Trends in Ecology and Evolution 18:411–417.

SAIKI, R. K., ET AL. 1988. Primer-directed enzymatic amplifications of DNA with thermostable DNA polymerase. Science 239:487–491.

SIMMONS, N. B. 2005. Order Chiroptera. Pp. 312–529 in Mammals species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.

SMITH, J. M., AND N. H. SMITH. 2002. Recombination in animal mitochondrial DNA. Molecular Biology and Evolution 19:2330–2332.

SMITH, M. F., AND J. L. PATTON. 1993. The diversification of South American murid rodents: evidence from the mitochondrial DNA sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50:149–177.

SPIX, J. DE. 1823. Simiarum et vespertilionum brasiliensium species novae, ou histoire naturelle des espèces nouvelles de singes et de chauves-souris observées et recueillies pendant le voyage dans l'intérieur du Brésil execute par ordre de S.M. le Roi de Bavière dans les années 1817, 1818, 1819, 1820. Francisci Seraphici Hübschmanni, Munich, Germany. Vol. 4.

STUDIER, E. H., AND D. E. WILSON. 1991. Physiology. Pp. 9–18 in Demography and natural history of the common fruit bat *Artibeus jamaicensis* on Barro Colorado Island, Panama (C. O. Handley, Jr., D. R. Wilson, and A. L. Gardner, eds.). Smithsonian Institution Press, Washington, D.C.

SWOFFORD, D. L. 2002. PAUP*: phylogenetic analysis using parsimony (* and other methods). Version 4.0b10. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

TANDLER, B., T. NAGATO, AND C. J. PHILLIPS. 1986. Systematic implications of comparative ultrastructure of secretory acini in the submandibular salivary gland in *Artibeus* (Chiroptera: Phyllostomidae). Journal of Mammalogy 67:81–90.

TUTTLE, M. D. 1970. Distribution and zoogeography of Peruvian bats, with comments on natural history. Univeristy of Kansas Science Bulletin 49:45–86.

VAN DEN BUSSCHE, R. A., J. L. HUDGEONS, AND R. J. BAKER. 1998. Phylogenetic accuracy, stability, and congruence: relationships within and among the New World bat genera *Artibeus*, *Dermanura*, and *Koopmania*. Pp. 59–71 in Bat biology and conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.

WETTERER, A. L., M. V. ROCKMAN, AND N. B. SIMMONS. 2000. Phylogeny of phyllostomid bats (Mammalia: Chiroptera): data from diverse morphological systems, sex chromosomes, and restriction sites. Bulletin of the American Museum of Natural History 248:1–200.

WILEY, E. O. 1978. The Evolutionary Species Concept reconsidered. Systematic Zoology 27:17–29.

WOLOSZYN, B. W., AND G. SILVA-TABOADA. 1977. Nueva especie fosil de *Artibeus* (Mammalia: Chiroptera) de Cuba, y tipificacion preliminar de los depósitos fosilíaferos Cubanos contentivos de mamíferos terrestres. Poeyana (Instituto de Zoologia, Academia de Ciencias de Cuba) 161:1–17.

Submitted 21 April 2006. Accepted 2 January 2007.

Associate Editor was Jesús E. Maldonado.

APPENDIX I

Taxa, geographic localities, haplotype codes, tissue and voucher numbers, and GenBank accession numbers of cytochrome-*b* sequences used for phylogenetic analysis. Haplotype codes follow subspecies identifications: aeq = *aequatorialis*, fal = *fallax*, gre = *grenadensis*, her = *hercules*, jam = *jamaicensis*, par = *parvipes*, pau = *paulus*, pla = *planirostris*, ric = *richardsoni*, tri = *trinitatus*, trio = *triomylus*, and yuc = *yucatanicus*. sch = *Artibeus schwartzi*. ACUNHC = Abilene Christian University Natural History Collection; CM = Carnegie Museum of Natural History; MVZ = Museum of Vertebrate Natural History; ROM = Royal Ontario Museum; TK (tissue number) and TTU (voucher number) = Natural Science Research Laboratory, Museum of Texas Tech University; and QCAZ = the Museo de Zoologia, Pontificia Universidad Católica del Ecuador.

Taxa	Locality	Haplotype	Tissue no.	Voucher no.	Accession no.
Koopmania concolor	Brokopondo, Suriname	—	TK 10378	CM 63792	L19515[a]
Dermanura bogotensis	Merida, Venezuela	—	TK 19381	CM 78459	DQ869386
D. phaeotis	Atlantida, Honduras	—	TK 136188	TTU 103810	DQ869387
Artibeus inopinatus	Valle, Honduras	—	TK 40184	TTU 61115	U66501[a]
A. hirsutus	Jalisco, Mexico	—	TK 48602	TTU 75563	AY684761[b]
A. hirsutus	Jalisco, Mexico	—	TK 48623	TTU 75562	AY684759[b]
A. fraterculus	El Oro, Ecuador	—	TK 135408	TTU 102476	DQ869388
A. fraterculus	Guayas, Ecuador	—	TK 134686	TTU 103519	DQ869389
A. obscurus	Pastaza, Ecuador	—	TK 104001	TTU 84773	DQ869392
A. obscurus	Potaro, Guyana	—	F 40891	ROM 109345	AF423079[c]
A. lituratus	Esmeraldas, Ecuador	—	TK 104525	TTU 85297	DQ869393
A. lituratus	Trinidad, Trinidad and Tobago	—	TK 25029	—	U66505[a]
A. fimbriatus	Canindeyu, Paraguay	—	TK 56670	TTU 94457	DQ869390
A. fimbriatus	San Pedro, Paraguay	—	TK 99588	TTU 96431	DQ869391
A. amplus	Amazonas, Venezuela	—	—	ROM 107904	AY642924[d]
A. amplus	Amazonas, Venezuela	—	—	ROM 107847	AY642923[d]
A. jamaicensis aequatorialis	El Oro, Ecuador	aeq 1	TK 135391	TTU 102771	DQ869440
A. jamaicensis aequatorialis	Guayas, Ecuador	aeq 2	TK 134602	TTU 103692	DQ869441
A. jamaicensis aequatorialis	Esmeraldas, Ecuador	aeq 3	TK 104686	TTU 85458	DQ869442
A. jamaicensis aequatorialis	Guayas, Ecuador	aeq 4	TK 134599	TTU 103689	DQ869443
A. jamaicensis aequatorialis	Esmeraldas, Ecuador	aeq 5	TK 104647	TTU 85419	DQ869444
A. jamaicensis aequatorialis	Guayas, Ecuador	aeq 6	TK 134600	TTU 103690	DQ869445
A. jamaicensis aequatorialis	Guayas, Ecuador	aeq 7	TK 134606	TTU 103696	DQ869446
A. jamaicensis aequatorialis	Esmeraldas, Ecuador	aeq 8	TK 104637	TTU 85409	DQ869447
A. jamaicensis aequatorialis	Esmeraldas, Ecuador	aeq 9	TK 104646	TTU 85418	DQ869448
A. jamaicensis aequatorialis	El Oro, Ecuador	aeq 10	TK 135106	TTU 102718	DQ869449
A. jamaicensis aequatorialis	Esmeraldas, Ecuador	aeq 11	TK 104512	TTU 85284	DQ869450
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117686	TTU 101657	DQ869457
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117651	TTU 101682	DQ869458
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117652	TTU 101683	DQ869459
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117653	TTU 101684	DQ869460
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117656	TTU 101687	DQ869461
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117687	TTU 101658	DQ869462
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117688	TTU 101659	DQ869463
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117689	TTU 101660	DQ869464
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117690	TTU 101661	DQ869465
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 1	TK 117691	TTU 101662	DQ869466
A. j. jamaicensis	Barbuda, Antigua and Barbuda	jam 1	TK 117629	TTU 101758	DQ869472
A. j. jamaicensis	Barbuda, Antigua and Barbuda	jam 1	TK 117630	TTU 101759	DQ869468
A. j. jamaicensis	Barbuda, Antigua and Barbuda	jam 1	TK 117631	TTU 101760	DQ869473
A. j. jamaicensis	Barbuda, Antigua and Barbuda	jam 1	TK 117632	TTU 101761	DQ869469
A. j. jamaicensis	Barbuda, Antigua and Barbuda	jam 1	TK 117633	TTU 101762	DQ869470
A. j. jamaicensis	Barbuda, Antigua and Barbuda	jam 1	TK 117634	TTU 101763	DQ869471
A. j. jamaicensis	Carriacou, St. Vincent and the Grenadines	jam 1	TK 18704	CM 63360	DQ869477
A. j. jamaicensis	St. Paul, Dominica	jam 1	TK 15522	TTU 31375	DQ869476
A. j. jamaicensis	St. Paul, Dominica	jam 1	TK 15519	TTU 31372	DQ869475
A. j. jamaicensis	St. Anns, Jamaica	jam 1	TK 27682	TTU 45295	DQ869480
A. j. jamaicensis	Quintana Roo, Mexico	jam 1	TK 82849	—	DQ869482
A. j. jamaicensis	Quintana Roo, Mexico	jam 1	TK 82850	—	DQ869481
A. j. jamaicensis	Montserrat	jam 1	TK 125175	—	DQ869487
A. j. jamaicensis	Montserrat	jam 1	TK 125176	—	DQ869488
A. j. jamaicensis	Nevis, St. Kitts and Nevis	jam 1	TK 125128	—	DQ869489
A. j. jamaicensis	Nevis, St. Kitts and Nevis	jam 1	TK 125129	—	DQ869490
A. j. jamaicensis	Nevis, St. Kitts and Nevis	jam 1	TK 125130	—	DQ869491
A. j. jamaicensis	Nevis, St. Kitts and Nevis	jam 1	TK 125133	—	DQ869492
A. j. jamaicensis	Nevis, St. Kitts and Nevis	jam 1	TK 125138	—	DQ869493
A. j. jamaicensis	Puerto Rico	jam 1	TK 21793	TTU 46370	DQ869494

APPENDIX I.—Continued.

Taxa	Locality	Haplotype	Tissue no.	Voucher no.	Accession no.
A. j. jamaicensis	Saba, Netherlands Antilles	jam 1	TK 117542	TTU 101955	DQ869496
A. j. jamaicensis	Saba, Netherlands Antilles	jam 1	TK 117543	TTU 101956	DQ869497
A. j. jamaicensis	Saba, Netherlands Antilles	jam 1	TK 117544	TTU 101957	DQ869498
A. j. jamaicensis	Saba, Netherlands Antilles	jam 1	TK 117545	TTU 101958	DQ869499
A. j. jamaicensis	Saba, Netherlands Antilles	jam 1	TK 117546	TTU 101959	DQ869500
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117573	TTU 102005	DQ869507
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117575	TTU 102007	DQ869501
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117576	TTU 102008	DQ869502
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117578	TTU 102010	DQ869503
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117579	TTU 102011	DQ869504
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117580	TTU 102012	DQ869508
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117581	TTU 102013	DQ869505
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117582	TTU 102014	DQ869509
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117584	TTU 102055	DQ869510
A. j. jamaicensis	Sint Eustatius, Netherlands Antilles	jam 1	TK 117587	TTU 102058	DQ869506
A. j. jamaicensis	St. Kitts, St. Kitts and Nevis	jam 1	TK 125143	—	DQ869511
A. j. jamaicensis	St. Kitts, St. Kitts and Nevis	jam 1	TK 125144	—	DQ869512
A. j. jamaicensis	St. Kitts, St. Kitts and Nevis	jam 1	TK 125145	—	DQ869513
A. j. jamaicensis	St. Kitts, St. Kitts and Nevis	jam 1	TK 125150	—	DQ869514
A. j. jamaicensis	Sint Maarten, Netherlands Antilles	jam 1	TK 117533	TTU 102081	DQ869516
A. j. jamaicensis	Sint Maarten, Netherlands Antilles	jam 1	TK 117535	TTU 102083	DQ869517
A. j. jamaicensis	Sint Maarten, Netherlands Antilles	jam 1	TK 117538	TTU 102079	DQ869518
A. j. jamaicensis	Antigua, Antigua and Barbuda	jam 2	TK 117654	TTU 101685	DQ869467
A. j. jamaicensis	St. Kitts, St. Kitts and Nevis	jam 2	TK 125142	—	DQ869515
A. j. jamaicensis	St. Anns, Jamaica	jam 3	TK 27688	TTU 45300	DQ869479
A. j. jamaicensis	Montserrat	jam 4	TK 125172	—	DQ869485
A. j. jamaicensis	Montserrat	jam 4	TK 125173	—	DQ869486
A. j. jamaicensis	Puerto Rico	jam 5	TK 21794	TTU 46371	DQ869495
A. j. parvipes	Guantanamo, Cuba	par 1	TK 32057	TTU 52549	DQ869474
A. j. paulus	Chiapas, Mexico	pau 1	—	—	AY382786[e]
A. j. paulus	San Salvador, El Salvador	pau 2	TK 34737	TTU 62441	DQ869455
A. j. paulus	San Salvador, El Salvador	pau 3	TK 34736	TTU 62440	DQ869456
A. j. richardsoni	Atlantida, Honduras	ric 1	TK 101381	TTU 84040	DQ869451
A. j. richardsoni	Atlantida, Honduras	ric 2	TK 101763	TTU 84420	DQ869452
A. j. richardsoni	Atlantida, Honduras	ric 3	TK 101764	TTU 84421	DQ869453
A. j. richardsoni	Copan, Honduras	ric 4	TK 101825	TTU 84482	DQ869454
A. j. richardsoni	Chiapas, Mexico	ric 5	—	—	AY382785[e]
A. j. richardsoni	Panama	ric 6	—	—	AY382784[e]
A. j. triomylus	Nayarit, Mexico	trio 1	—	—	AY144344[e]
A. j. triomylus	Guerrero, Mexico	trio 2	—	—	AY144342[e]
A. j. triomylus	Colima, Mexico	trio 3	—	—	AY144345[e]
A. j. triomylus	Morelos, Mexico	trio 4	—	—	AY144346[e]
A. j. triomylus	Colima, Mexico	trio 5	—	—	AY382782[e]
A. j. yucatanicus	Quintana Roo, Mexico	yuc 1	TK 82854	—	DQ869484
A. j. yucatanicus	Roatan Island, Honduras	yuc 1	TK 82863	—	DQ869478
A. j. yucatanicus	Quintana Roo, Mexico	yuc 2	TK 82853	—	DQ869483
A. j. yucatanicus	Veracruz, Mexico	yuc 3	—	—	AY144340[e]
A. planirostris fallax	French Guiana	fal 1	TK 143051	CM 83901	DQ869398
A. planirostris fallax	La Paz, Bolivia	fal 2	TK 14535	TTU 34863	AY684718[b]
A. planirostris fallax	La Paz, Bolivia	fal 3	TK 14536	TTU 34864	AY684723[b]
A. planirostris fallax	French Guiana	fal 4	TK 18788	AMNH 267202	U66503[a]
A. planirostris fallax	Bolivar, Venezuela	fal 5	TK 19025	—	DQ869426
A. planirostris fallax	Amazonas, Venezuela	fal 6	—	ACUNHC 290	AY642915[d]
A. planirostris fallax	Amazonas, Venezuela	fal 7	—	ACUNHC 291	AY642913[d]
A. planirostris fallax	Amazonas, Venezuela	fal 8	—	ROM 107888	AY642914[d]
A. planirostris fallax	Amazonas, Venezuela	fal 9	—	ACUHNC 292	AY642917[d]
A. p. hercules	Napo, Ecuador	her 1	TK 125293	QCAZ 5182	DQ869399
A. p. hercules	Napo, Ecuador	her 2	TK 125294	QCAZ 5183	DQ869400
A. p. hercules	Napo, Ecuador	her 3	TK 125296	QCAZ 5186	DQ869414
A. p. hercules	Napo, Ecuador	her 4	TK 125300	QCAZ 5191	DQ869401
A. p. hercules	Napo, Ecuador	her 5	TK 125303	QCAZ 5194	DQ869415
A. p. hercules	Napo, Ecuador	her 6	TK 125304	QCAZ 5195	DQ869413
A. p. hercules	Sucumbios, Ecuador	her 7	TK 125307	QCAZ 6862	DQ869411
A. p. hercules	Sucumbios, Ecuador	her 8	TK 125306	QCAZ 6913	DQ869412

APPENDIX I.—Continued.

Taxa	Locality	Haplotype	Tissue no.	Voucher no.	Accession no.
A. p. hercules	Pastaza, Ecuador	her 9	TK 104002	TTU 84774	DQ869402
A. p. hercules	Pastaza, Ecuador	her 10	TK 104004	TTU 84776	DQ869403
A. p. hercules	Pastaza, Ecuador	her 11	TK 104005	TTU 84777	DQ869404
A. p. hercules	Pastaza, Ecuador	her 12	TK 104016	TTU 84788	DQ869407
A. p. hercules	Pastaza, Ecuador	her 13	TK 104017	TTU 84789	DQ869408
A. p. hercules	Pastaza, Ecuador	her 14	TK 104332	TTU 85104	DQ869405
A. p. hercules	Pastaza, Ecuador	her 15	TK 104404	TTU 85176	DQ869409
A. p. hercules	Pastaza, Ecuador	her 16	TK 104410	TTU 85182	DQ869410
A. p. hercules	Pastaza, Ecuador	her 17	TK 104411	TTU 85183	DQ869416
A. p. hercules	Pastaza, Ecuador	her 18	TK 104413	TTU 85185	DQ869417
A. p. hercules	Pastaza, Ecuador	her 19	TK 104414	TTU 85186	DQ869406
A. p. hercules	Pastaza, Ecuador	her 20	TK 104419	TTU 85191	DQ869418
A. p. hercules	Madre de Dios, Peru	her 21	TK 16633	MVZ 170016	U66508[a]
A. p. hercules	Madre de Dios, Peru	her 22	TK 16634	—	DQ869397
A. p. hercules	Huanuco, Peru	her 23	TK 22626	TTU 46245	AY684724[b]
A. p. hercules	Huanuco, Peru	her 24	TK 22629	TTU 46247	AY684716[b]
A. p. hercules	Cuzco, Peru	her 25	—	MVZ 166536	AY684726[b]
A. p. hercules	Cuzco, Peru	her 26	—	MVZ 166539	AY684725[b]
A. p. hercules	Madre de Dios, Peru	her 27	—	MVZ 168918	AY684743[b]
A. p. planirostris	San Pedro, Paraguay	pla 1	TK 56621	TTU 95788	DQ869396
A. p. planirostris	San Pedro, Paraguay	pla 2	TK 56656	TTU 96811	DQ869394
A. p. planirostris	Concepcion, Paraguay	pla 3	TK 64198	TTU 99479	DQ869395
A. p. planirostris	Concepcion, Paraguay	pla 4	TK 64251	TTU 99520	AY684775[b]
A. p. planirostris	Bahia, Brazil	pla 5	—	MVZ 185497	AY684776[b]
A. p. planirostris	Paraiba, Brazil	pla 6	—	MVZ 185790	AY684744[b]
A. p. trinitatis	Guarico, Venezuela	tri 1	TK 15011	TTU 33331	DQ869423
A. p. trinitatis	Guarico, Venezuela	tri 2	TK 15012	TTU 33332	DQ869422
A. p. trinitatis	Guarico, Venezuela	tri 3	TK 15013	TTU 33333	DQ869424
A. p. trinitatis	Guarico, Venezuela	tri 4	TK 15020	TTU 33340	DQ869425
A. p. trinitatis	Trinidad, Trinidad and Tobago	tri 5	TK 25026	TTU 44060	DQ869432
A. p. trinitatis	Trinidad, Trinidad and Tobago	tri 6	TK 25085	TTU 44061	DQ869433
A. p. trinitatis	Tobago, Trinidad and Tobago	tri 7	TK 25185	TTU 44046	DQ869427
A. p. trinitatis	Tobago, Trinidad and Tobago	tri 7	TK 25187	TTU 44048	DQ869431
A. p. trinitatis	Tobago, Trinidad and Tobago	tri 7	TK 25188	TTU 44049	DQ869428
A. p. trinitatis	Tobago, Trinidad and Tobago	tri 7	TK 25203	TTU 44057	DQ869429
A. p. grenadensis	St. George, Grenada	tri 7	TK 18520	CM 63322	DQ869435
A. p. grenadensis	St. George, Grenada	tri 7	TK 18522	CM 63324	DQ869437
A. p. grenadensis	St. George, Grenada	tri 7	TK 18527	CM 63329	DQ869438
A. p. grenadensis	St. George, Grenada	tri 7	TK 18530	CM 63332	DQ869439
A. p. grenadensis	Carriacou, St. Vincent and the Grenadines	tri 7	TK 18654	CM 63369	DQ869434
A. p. trinitatus	Tobago, Trinidad and Tobago	tri 8	TK 25186	TTU 44047	DQ869430
A. p. grenadensis	St. George, Grenada	tri 8	TK 18528	CM 63330	DQ869436
A. schwartzi	Carriacou, St. Vincent and the Grenadines	sch 1	TK 18705	CM 63361	DQ869519
A. schwartzi	St. Kitts, St. Kitts and Nevis	sch 1	TK 125147	—	DQ869522
A. schwartzi	Nevis, St. Kitts and Nevis	sch 1	TK 125139	—	DQ869521
A. schwartzi	Montserrat	sch 1	TK 125174	—	DQ869520
A. schwartzi	St. Vincent, St. Vincent and the Grenadines	sch 1	TK 82838	CM 83208	DQ869528
A. schwartzi	St. Vincent, St. Vincent and the Grenadines	sch 1	TK 82839	CM 83210	DQ869524
A. schwartzi	St. Vincent, St. Vincent and the Grenadines	sch 1	TK 82840	CM 83212	DQ869529
A. schwartzi	St. Vincent, St. Vincent and the Grenadines	sch 1	TK 82841	CM 83213	DQ869526
A. schwartzi	St. Vincent, St. Vincent and the Grenadines	sch 1	TK 82843	CM 83219	DQ869530
A. schwartzi	St. Vincent, St. Vincent and the Grenadines	sch 1	TK 82844	CM 83221	DQ869531
A. schwartzi	St. Vincent, St. Vincent and the Grenadines	sch 1	TK 82846	CM 83224	DQ869527
A. schwartzi	St. Vincent, St. Vincent and the Grenadines	sch 2	TK 82842	CM 83218	DQ869525
A. schwartzi	Barinas, Venezuela	sch 3	TK 19492	CM 78478	DQ869523

[a] Sequences from Van Den Bussche et al. (1998).
[b] Sequences from Guerrero et al. (in litt.).
[c] Sequences from Davalos and Jansa (2004).
[d] Sequences from Lim et al. (2004).
[e] Sequences from Guerrero et al. (2004).