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TAXONOMIC STATUS OF *ARTIBEUS JAMAICENSIS TRIOMYLUS* INFERRED FROM MOLECULAR AND MORPHOMETRIC DATA

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The taxonomic status of *Artibeus jamaicensis triomylus* was evaluated by mitochondrial cytochrome-*b* sequences, as well as cranial morphometric comparisons with 4 other subspecies of the *A. jamaicensis* complex and 5 species of large *Artibeus*. Phylogenetic analyses showed that 2 monophyletic groups exist within *A. jamaicensis* complex, separated by a sequence divergence of 3.6%. One clade grouped samples of *A. j. triomylus* from western Mexico, and the other contained samples of *A. j. yucatanicus*, *A. j. richardsoni*, *A. j. paulus*, and *A. j. jamaicensis* from the Gulf of Mexico, Central America, and the Caribbean. Additionally, multivariate analyses revealed a significant divergence in quantitative cranial characters between *A. j. triomylus* and non-*triomylus* specimens. These results, in conjunction with morphological data previously reported, suggest that *A. j. triomylus* represents a distinct and monophyletic lineage, consequently deserving recognition at the species rank.

Key words: *Artibeus*, cytochrome *b*, morphometrics, phylogeny, species concept, taxonomy

Recent taxonomic studies have provided a new perspective on the systematics of the once continentally widespread *A. jamaicensis* complex. Lim (1997), based on multivariate analysis of craniometric data, concluded that *A. planirostris* is a distinct species instead of a subspecies of *A. jamaicensis*, as had been treated previously by Hershkovitz (1949) and Handley (1987). Alternatively, Phillips et al. (1991) and Pumo et al. (1996) found that *A. jamaicensis* from Central America and the Caribbean and *A. planirostris* from French Guiana and the Lesser Antillean island of St. Vincent represent 2 lineages that are characterized by different mitochondrial DNA haplotypes. Likewise, a recent phylogenetic analysis based on molecular and morphometric data indicated *A. planirostris* and *A. jamaicensis* are not conspecific, because the former was found to be more closely related to *A. obscurus* rather than to *A. jamaicensis* (Guerrero et al. 2003). This taxonomic arrangement restricted the geographic distribution of *A. jamaicensis* from western Ecuador and northern Venezuela to northern Mexico, including Greater and Lesser Antilles (Hall 1981; Koopman 1993).

Morphological variability among populations of *A. jamaicensis* is remarkable, and had led to the recognition of 8 subspecies differing primarily in characters such as size, color, and number of upper molars (Davis 1970; Hall 1981; Jones and Phillips 1970; Koopman 1978). *A. j. triomylus* is perhaps the most distinctive subspecies in the northern range of the *A. jamaicensis* complex. This taxon was described by Handley (1966) based on cranial characters that distinguish it from the contiguous subspecies *A. j. yucatanicus*. In a review of the *A. jamaicensis* complex from Middle America (Davis 1970), *A. j. triomylus* was confirmed as consisting of populations with 3/3 molars in contrast to the 2/3 condition usually found elsewhere in the area. Conclusions of Davis (1970) lead to the interpretation that Mexican populations with 3/3 molars were disjunct relative to other 3/3 populations (*A. j. trinitatis*) from Colombia and Venezuela (Koopman 1978).

Herein the taxonomic status of populations traditionally assigned to *A. j. triomylus* is assessed by applying the phylogenetic species concept (sensu Mishler and Brandon 1987). Guided by this concept, we carried out a 2-fold approach designed to determine monophyly and provide criteria for ranking. First, a cladistic analysis of complete sequences of the mitochondrial cytochrome-*b* gene (*Cytb*) was conducted to examine the phylogenetic relationships of populations of *A. jamaicensis* assigned to 5 subspecies from Mexico, Central America, and the Caribbean and 5 other species of large *Artibeus*, and to assess levels of genetic differentiation within and among taxa. Second, we analyzed morphometric variation and disparity within and among clades detected in the cladistic analysis with multivariate analysis. These analyses were used

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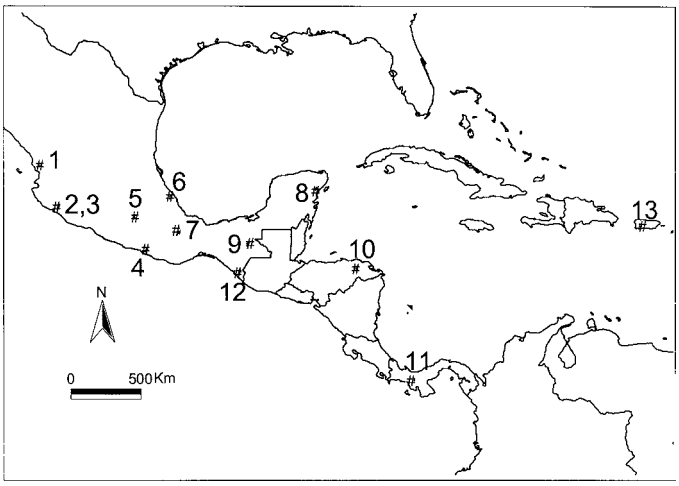

FIG. 1.—Collection localities of the 13 specimens of *Artibeus jamaicensis* complex included in the phylogenetic analysis. Numbers represent the localities indicated in Appendix I.

to emphasize the morphometric distinction among subspecies of *A. jamaicensis*.

MATERIALS AND METHODS

Samples.—We downloaded 8 sequences of *Cytb* from GenBank. In addition, we isolated DNA from 15 tissue samples loaned from collaborative institutions or colleges. Thirteen samples (Fig. 1; Appendix I) represented 5 subspecies of *A. jamaicensis* complex: *A. j. triomylus* (Nayarit, Colima, Morelos, and Guerrero, Mexico), *A. j. yucatanicus* (Veracruz, Oaxaca, and Quintana Roo, Mexico), *A. j. richardsoni* (Chiapas, Mexico; Honduras; and Panama), *A. j. paulus* (Chiapas, Mexico), and *A. j. jamansis* (Puerto Rico). Nine samples of non-*jamaicensis* taxa were used as reference, and *Dermanura azteca* and *D. tolteca* were included as outgroups.

DNA Sequencing.—Mitochondrial DNA was extracted from liver or kidney tissue following a protocol modified from González and Vovides (2002). Polymerase chain reaction (PCR) methods were used to amplify the complete *Cytb* gene using primers L14724 and H15915R (Irwin et al. 1991). PCR amplification conditions were initial template denaturation for 3 min at 94°C followed by 30 cycles of 30 s denaturation at 94°C, 30 s annealing at 55°C, and 30 s extension at 72°C, and a final extension of 6 min at 72°C. PCR products were purified with Gene Clean III (Bio 101 Inc., Vista, California) following the procedure recommended by the manufacturer, and resuspended in 20 μl of autoclaved water. Amplified DNA was sequenced using a Big Dye Terminator Mix (Applied Biosystems, Inc., Warrington, England) as described by the manufacturers. PCR cycle sequencing conditions were initial template denaturation for 4 min at 96°C followed by 25 cycles of 30 s denaturation at 96°C, 15 s annealing at 50°C, and 4 min extension at 60°C. Sequencing products were run on a 4.75% polyacrylamide gel using an ABI-373A automated sequencer (Perkin-Elmer, Inc., Foster City, California).

Phylogenetic analysis.—Sequences were aligned by eye and proofed by translating into amino acid sequences using McClade 3.04 (Maddison and Maddison 1992). A phylogenetic reconstruction was obtained by parsimony and maximum likelihood approaches implemented in PAUP* (version 4.0b10—Swofford 2002). For parsimony analysis we used the branch and bound algorithm, with informative nucleotide positions treated as unordered, discrete characters with 4 possible character states, and with equal weight. For maximum likelihood analysis, the computer program ModelTest (version 3.0—Posada and Crandall 1998) was used to statistically compare successively nested models and to determine the appropriate model of sequence evolution for this data set. Due to computational difficulty, this analysis was carried out with a heuristic search with 100 random sequence addition replicates, and tree bisection and reconnection branch swapping.

We used parsimony bootstrapping as a measure of clade support (Felsenstein 1985), and Bayesian posterior probabilities as a measure of reliability of clades (Huelsenbeck et al. 2002). Parsimony bootstrapping was computed with 1,000 bootstrap iterations and a heuristic search with 10 sequence additions. Bayesian posterior probabilities were generated with MrBayes 2.0 (Huelsenbeck and Ronquist 2001) using Marcov chain Monte Carlo with the Metropolis-Hasting algorithm. No a priori assumptions about topology were made, and all searches were provided with uniform priors. Two separate runs were performed to assure the coverage of tree space. Each search was run for 1,000,000 generations and every 100th tree was sampled. Burn-in value was determined when negative log-likelihood (−lnL) values reached an asymptote. Posterior probabilities for each clade were computed by a majority consensus tree after burn-in (1,000 trees excluded).

Quantitative pairwise comparisons were made using genetic distances corrected for the Kimura 2-parameter model of evolution (K2P—Kimura 1980). This model was selected to allow for comparisons to other molecular studies of phyllostomid bats as a general measure for establishing taxonomic rank (Bradley and Baker 2001).

Morphometric analyses.—We examined 545 adult specimens representing 5 subspecies of *A. jamaicensis* complex and its congeners (Appendix II). Adults were classified based on complete ossification of phalanges. Skulls and jaws were digitized with a Mavica-FD88 (Sony Corporation, Japan) camera, using a spirit level to assure that the lens and the specimen plane were parallel. Digital images were measured with computer program Image-Pro Plus (Media Cybernetics 1994). Sixteen cranial characters were included: length of skull, excluding incisors; condylobasal length, excluding incisors; mastoidal breadth; breadth of braincase; zygomatic breadth; postorbital constriction; breadth across postorbital process; breadth across upper 1st molars; breadth across upper canines; breadth of pterygoid fossa; palatal length, taken from anterior-most point of pterygoid fossa to posterior-most point of incisive foramen; breadth of palate, taken as distance between internal margin of upper 2nd molars; length of mandible; length of mandibular toothrow; height of coronoid process, taken from the dorsal-most point on ventral border of horizontal ramus to tip of coronoid process; and breadth of masseteric region, taken from the anterior-most point of coronoid process to the posterior-most point of condylar process.

Descriptive statistics (mean, *SD*, and range) for each character were calculated for comparative purposes (available upon request). Data were log-transformed to meet assumptions of normality and linear relationships among variables, as required by analytical methods. Secondary sexual dimorphism was evaluated using a multivariate analysis of variance (MANOVA) to determine if individuals from both sexes could be pooled for between-group comparisons. Multivariate variation across taxa was assessed by principal component analysis (PCA) based on variance-covariance matrix. A discriminant function analysis was performed to examine multivariate differentiation among a priori designated groups and to identify which characters were more useful in detecting these differences. Squared Mahalanobis distances (D^2) were calculated from pairwise comparisons as a measure of morphometric divergence among taxa examined (Sneath and Sokal

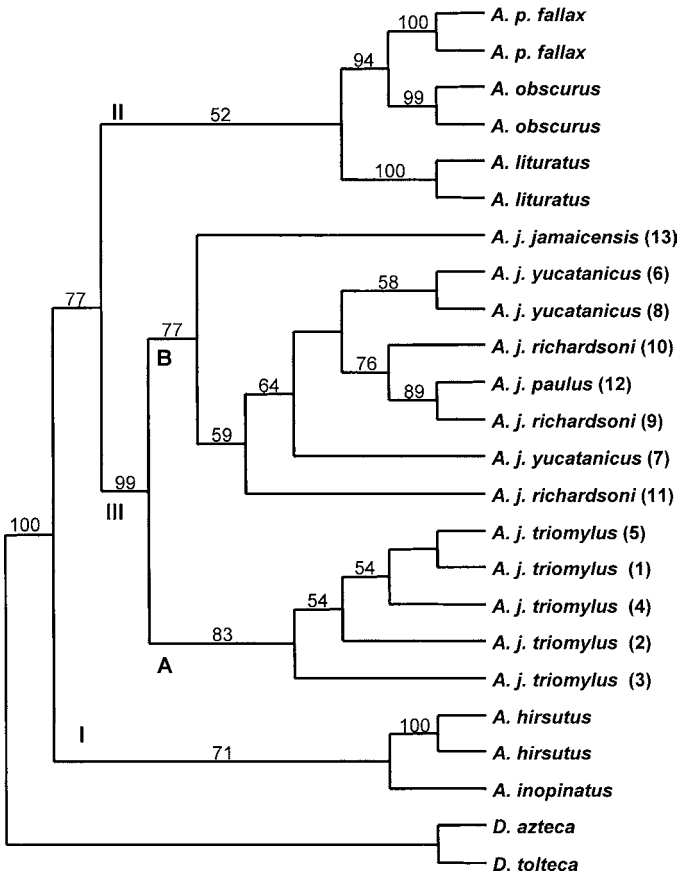

FIG. 2.—Most parsimonious tree (length = 612, consistency index = 0.578, and retention index = 0.688) depicting phylogenetic relationships among 22 samples of large *Artibeus* and 2 outgroups based on *Cytb* gene variation. Numbers above each branch represent parsimony bootstrap proportions, and numbers that follow taxon names correspond to the localities in Fig. 1 and Appendix I. Roman numerals and letters indicate major clades as defined in text.

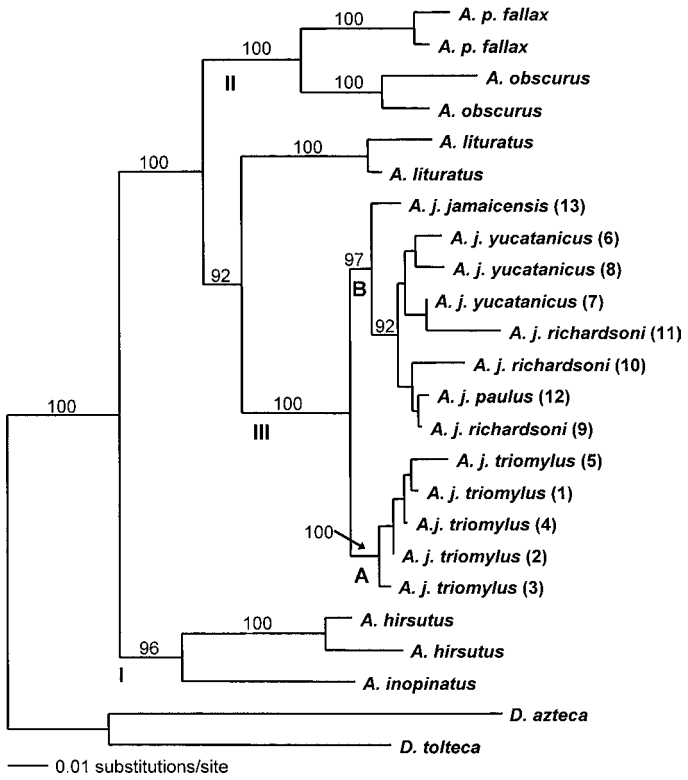

FIG. 3.—Maximum likelihood phylogram (−lnL = 4,513.2756) recovered using the TrN + I + Γ model of evolution. Numbers above branches represent Bayesian posterior probabilities as percent. Roman numerals and letters indicate major clades as defined in text.

1973). Statistical analyses were performed using Statistica 6 (StatSoft 1998), and NTSYS-pc 2.01 (Rohlf 1997).

RESULTS

Phylogenetic analysis.—We compiled a data matrix of 24 complete sequences of mitochondrial *Cytb* representing populations of 6 species of large *Artibeus* and 2 outgroups. Two hundred and two sites (23, 8, and 171, 1st, 2nd, and 3rd position, respectively) were parsimony informative. Parsimony analysis recovered 1 most-parsimonious tree (steps = 612, CI = 0.572, RI = 0.688). This topology (Fig. 2) depicted 3 major clades. Clade I contained samples of *A. hirsutus* and *A. inopinatus*. Clade II contained the samples of *A. lituratus*, *A. obscurus*, and *A. planirostris fallax*; these latter 2 species formed a sister relationship. Clade III included all samples of *A. jamaicensis*, which is further divided into 2 minor clades (A and B). Clade A included all samples of *A. j. triomylus*. Clade B contained samples of *A. j. yucatanicus*, *A. j. richardsoni*, *A. j. paulus*, and *A. j. jamaicensis*.

ModelTest determined the TrN + I + Γ as the model that best fits the data. Parameter estimates for this model were as follows: 1) base frequencies, A = 0.2903, C = 0.2922, T = 0.2871, and G = 0.1304; 2) rate matrix, [A–C] = 1, [A–G] = 4.25, [A–T] = 1, [C–G] = 1, [C–T] = 16.24, and [G–T] = 1; 3) I = 0.55; and 4) Γ = 1.48. The maximum likelihood search using that model found 1 tree (Fig. 3) with a −lnL of 4,513.2756. This tree differed from the parsimony tree in the position of *A. lituratus*, which under maximum likelihood analysis appeared as sister to the clade formed by samples of *A. jamaicensis* complex (clade III), as well as the relationships within clade formed by non-*triomylus* samples. Levels of support and reliability for the main clades were high, except the clade II in the parsimony analysis.

Genetic distances corrected by K2P model were averaged for comparisons within and among selected taxa or clades, and converted to percentages (Table 1). Genetic distances within subspecies of *A. jamaicensis* complex ranged from 0.3% (between 2 samples of *A. j. triomylus*) to 2.7% (between 2 samples of *A. j. richardsoni*). Genetic variation among subspecies also was low, ranging from 1.4% (between *A. j. richardsoni* and *A. j. yucatanicus*) to 4.3% (between *A. j. richardsoni* and *A. j. triomylus*). In contrast, level of genetic differentiation among species ranged from 7.9% (between *A. obscurus* and *A. p. fallax*) to 15.3% (between *A. j. richardsoni* and *A. hirsutus*).

Morphometric analyses.—Significant secondary sexual variation was found only for samples of *A. j. triomylus*, based on the MANOVA analysis ($P < 0.001$). Therefore, specimens of both sexes were pooled in subsequent analyses.

Table 1.—Average genetic distances corrected by Kimura-2 parameter model (Kimura 1980) for comparisons within and among selected taxa or clades recovered in phylogenetic analysis.

Comparisons	Average genetic distance (%)
Within *A. j. triomylus*	0.8
Within *yucatanicus-jamaicensis-paulus-richardsoni*	1.9
triomylus compared to *richardsoni*	4.3
triomylus compared to *yucatanicus*	3.9
triomylus compared to *jamaicensis*	3.0
triomylus compared to *paulus*	3.2
triomylus compared to *yucatanicus-jamaicensis-richardsoni-paulus*	3.6
triomylus compared to *hirsutus*	13.1
triomylus compared to *intermedius*	9.1
triomylus compared to *fallax*	11.1
triomylus compared to *obscurus*	11.9
triomylus compared to *inopinatus*	11.8
obscurus compared to *fallax*	7.9
inopinatus compared to *hirsutus*	10.5
hirsutus compared to *intermedius*	13.9

Principal component analysis established that 63.4% of the variation among taxa was attributable to size, as determined by high positive loadings of all characters on principal component 1 (Marcus 1990). Principal components 2 and 3 accounted for 7.6% and 6.0%, respectively. A 3-dimensional plot of the first 3 principal components (Fig. 4) illustrated that *A. lituratus*, *A. p. fallax*, and *A. obscurus* are the most distinct taxa on principal component space, with the remaining taxa mostly overlapping.

Differentiation among groups was achieved by discriminant function analysis. The 1st canonical variable expressed 41.7% of the morphometric variation and the 2nd canonical variable explained 20.4%. Plots of the first 2 canonical variates (Fig. 5a) depicted a poor morphometric differentiation among most taxa. *A. lituratus* and *A. p. fallax* were the most distinctive groups. When only samples of *A. jamaicensis* complex were analyzed by discriminant function analysis (Fig. 5b), the 1st and 2nd canonical variates accounted for 64.1% and 24.3% of the variation, respectively. *A. j. triomylus* and *A. j. jamaicensis* were the most distinctive taxa. Lack of discrimination was especially evident for *A. j. yucatanicus*, *A. j. richardsoni*, and *A. j. paulus*, whose centroids were encompassed by 95% confidence ellipses.

The greatest morphological divergence (Table 2) resulted from the comparison between *A. hirsutus* and *A. lituratus* ($D^2 = 77.3$), followed by the comparison between *A. j. jamaicensis* and *A. lituratus* ($D^2 = 69.9$). The shortest D^2 values were from comparisons between *A. j. richardsoni* and *A. j. paulus* ($D^2 = 3.4$).

Table 2.—Morphometric divergence between taxa examined as indicated by Mahalanobis distances (D^2).

	Taxa								
	1	2	3	4	5	6	7	8	9
1. *Artibeus jamaicensis triomylus*		14.8	15.4	36.4	16.3	22.8	45.9	38.1	38.0
2. *A. j. yucatanicus*			4.4	4.2	4.3	19.7	56.0	25.6	34.3
3. *A. j. richardsoni*				3.9	3.4	24.4	46.7	26.2	20.9
4. *A. j. jamaicensis*					4.1	41.7	69.8	38.8	30.4
5. *A. j. paulus*						22.5	52.4	23.6	29.9
6. *A. hirsutus*							77.3	48.4	64.0
7. *A. lituratus*								66.0	41.3
8. *A. obscurus*									51.4
9. *A. planirostris fallax*									

Discussion

Phylogenetic hypothesis recovered by parsimony and maximum likelihood revealed that 2 monophyletic clades exist within the *A. jamaicensis* complex. Clade A corresponded to samples of *A. j. triomylus* from western Mexico. Clade B contained samples of *A. j. yucatanicus*., *A. j. richardsoni*, *A. j. paulus*, and *A. j. jamaicensis* from the Gulf of Mexico, Central America, and the Caribbean. Both clades are well supported by parsimony bootstrapping and Bayesian posterior probabilities, although relationships of haplotypes within clade B differed in parsimony and maximum likelihood analyses. The average genetic distance within clade A was 0.8% (0.3–1.4%), and within clade B was 1.9% (1.3–2.5%). However, clade A differed from clade B by an average sequence divergence of 3.6% (2.9–5.1%). At this level of differentiation of *Cytb* gene, *A. j. triomylus* is as different from other *A. jamaicensis* as are other sister species in other phyllostomid genera. For example, genetic distance between *Carollia brevicauda* (sensu stricto) and *C. perspicillata* was 3.6% (Baker et al. 2002), between *Chiroderma doriae* and *C. trinitatum* was 3.2% (Baker et al. 1994), and between *Dermanura watsoni* and *D. azteca* was 4.8 (Van Den Bussche et al. 1998).

The substitution rate for mammalian *Cytb* varies from 3 to 5% per million years (Arbogast 1999). If we consider a mean of 4%, then we can presume that populations of clade A (*A. j. triomylus*) and populations of clade B (*A. j. yucatanicus*, *A. j richardsoni*, and *A. j. jamaicensis*) diverged from a common ancestor about 1×10^6 years ago. This hypothesis places the divergence time of both clades during the Pleistocene, a period characterized in Mexico by habitat expansion-retraction cycles in response to changes in climate, sea level, and glacial fronts (Toledo 1982). Such habitat fragmentation could have resulted in vicariant events that split the population occurring in the western Pacific region of Mexico from those occurring in Gulf of Mexico, Central America, and Caribbean areas. Similar patterns of distribution are shown by several endemic bats such as *Musonycteris harrisoni*, *Dermanura phaeotis nanus*, *Rhogeessa tumida*, and *Hylonycteris underwoodi minor* that inhabit the lowlands of western Mexico (Hall 1981). This region appears to be a well marked biogeographic unit that was isolated from the Pacific versant south of the Isthmus of Tehuantepec and from the Atlantic versant of Mexico (Davis 1970).

Multivariate analyses revealed that most taxa included are morphologically similar, regardless of specific or subspecific status. Principal component analysis suggested that size (PC1) accounted for most variation among taxa, with all samples of *A. jamaicensis* complex overlapping on this axis. These results do not support Davis' (1970) conclusion that subspecies of *A. jamaicensis* differ in size. Discriminant function analysis revealed that cranial morphology of *A. lituratus* and *A. p. fallax* are the most distinctive, compared

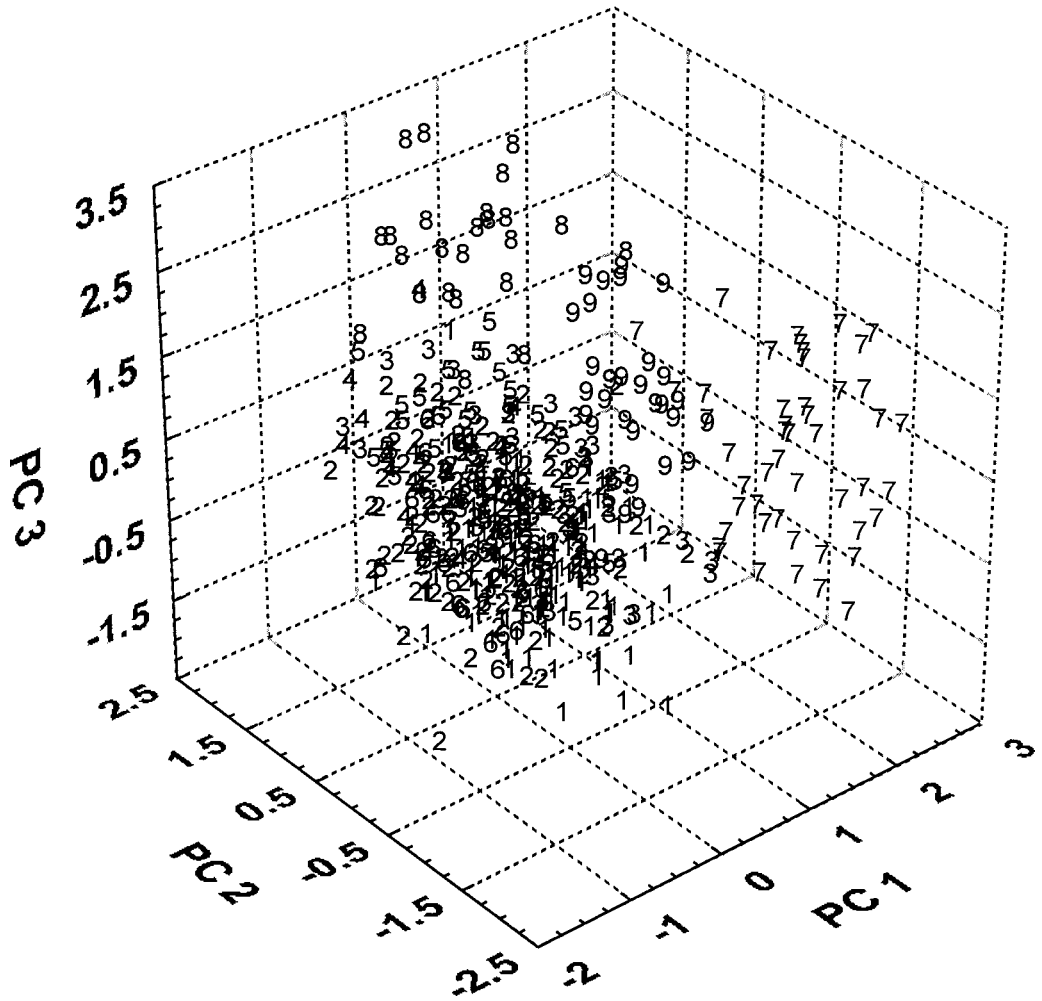

Fig. 4.—Scatterplot of the first 3 principal components showing scores, labeled to represent taxa as follows: 1) *Artibeus jamaicensis triomylus*, 2) *A. j. yucatanicus*, 3) *A. j. richardsoni*, 4) *A. j. jamaicensis*, 5) *A. j. paulus*, 6) *A. hirsutus*, 7) *A. lituratus*, 8) *A. obscurus*, and 9) *A. planirostris fallax*.

with other taxa. This analysis also indicated that specimens of *A. j. triomylus* are well distinguished from specimens of non-*triomylus* subspecies. In fact, the degree of cranial divergence (measured in terms of D^2 distance) among *A. j. triomylus* and any other *A. jamaicensis* subspecies is 3 times higher than the highest divergence observed between any of these subspecies (Table 2).

There are, in addition, other characters in which individuals of *A. j. triomylus* differ markedly from individuals belonging to *A. jamaicensis* complex. The presence of 3rd upper molars is the most reliable character that distinguishes this bat. Davis (1970) pointed out that 70 of 71 specimens of this subspecies possessed these molars, but only 10 specimens of 725 of other subspecies from throughout the remainder of Middle America exhibited this condition. In addition, Handley (1966) concluded that specimens belonging to *A. j. triomylus* differ from those of the contiguous subspecies *A. j. yucatanicus* in having the supraorbital edges converging sharply posteriorly, the post-orbital constriction positioned over the posterior edge of the suborbital shelf, and the 2nd lower molars wider.

Systematic conclusion.—The phylogenetic species concept implies that a species is the least inclusive taxon recognized in a formal phylogenetic classification (Mishler and Theriot 2000). This concept encompasses 2 theoretical components: grouping and ranking. First, specimens must be grouped into species on the basis of evidence of monophyly, as at all taxonomic levels. Second, ranking criteria used to assign species rank to certain monophyletic groups should vary among different organisms. These criteria have included genetic distances, morphological gaps, and presence of breeding barriers.

Our phylogenetic hypothesis inferred from *Cytb* sequences demonstrated that samples of *A. j. triomylus* form a robust monophyletic group, which is separated from the clade including non-*triomylus* subspecies by a genetic distance of 3.6%. This level of divergence is within the range of that reported among other closely related but clearly distinct species of phyllostomid bats. Consequently, we argue that monophyly of populations currently classified as subspecies *A. j. triomylus*, and the level of genetic divergence separating them from the remaining populations of *A. jamaicensis*, in concert with

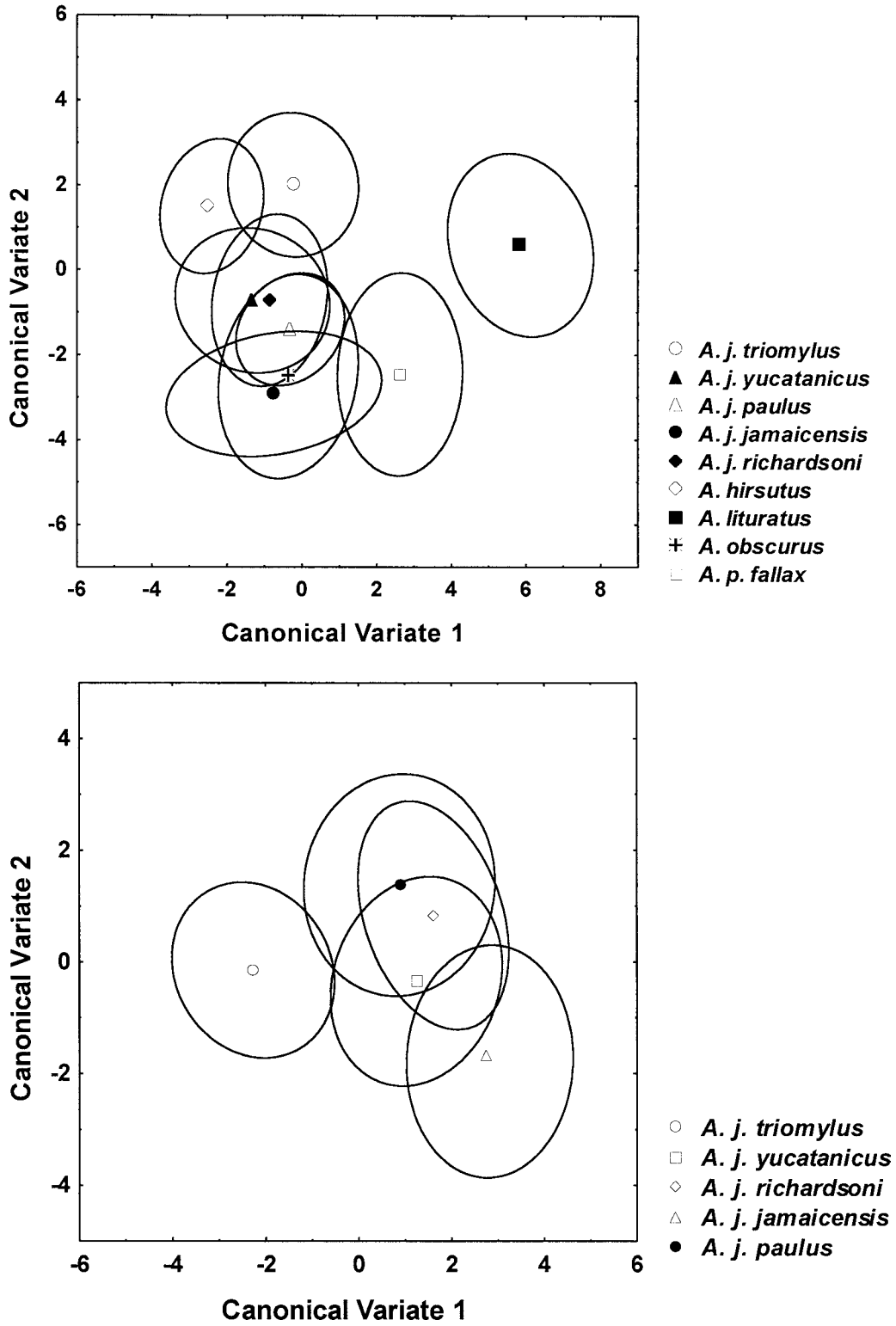

FIG. 5.—Plots of the first 2 canonical variates obtained from discriminant function analysis (DFA) of 16 cranial characters showing centroids and 95% confidence ellipses. A) DFA including all samples of large *Artibeus*; B) DFA including only samples of *A. jamaicensis* complex.

morphological distinctiveness of these bats, meet the requirements of the phylogenetic species concept. Thus, they deserve recognition at species rank as *A. triomylus*. This distinction better represents the evolutionary (genetic and morphological) divergence of this linage of large *Artibeus*.

RESUMEN

El estado taxonómico de *A. j. triomylus* fue evaluado por medio de comparaciones del gen mitocondrial citocromo b, así como comparaciones morfométricas con otros 6 taxa de *Artibeus* grandes. El análisis filogenético mostró la existencia

de 2 grupos monofiléticos dentro del complejo *A. jamaicensis*, separados por una divergencia genética de 3.6%. Un clado agrupó a las poblaciones de *A. j. triomylus* del oeste de México, y el otro a las poblaciones de *A. j. yucatanicus*, *A. j. richardsoni*, *A. j. paulus* y *A. j. jamaicensis* del Golfo de México, Centro América, y Caribe. Además, los análisis multivariados demostraron una divergencia significativa en los caracteres craneales cuantitativos entre los especimenes de *A. j. triomylus* y los no *triomylus*. Estos resultados, junto con los datos morfológicos reportados previamente, sugieren que *A. j. triomylus* representa un linaje monofilético distinto, y en consecuencia merece el reconocimiento al rango de especie.

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Literature Cited

Arbogast, B. S. 1999. Mitochondrial DNA phylogeography of the New World flying squirrels (*Glaucomys*): implications for Pleistocene biogeography. Journal of Mammalogy 80:142–155.

Baker, R. J., S. Solari, and F. Hoffmann. 2002. A new Central America species from the *Carollia brevicauda* complex. Occasional Papers, Museum of Texas Tech University 217:1–12.

Baker, R. J., A. A. Taddei, J. L. Hudgeons, and R. A. Van Den Bussche. 1994. Systematic relationships within *Chiroderma* (Chiroptera: Phyllostomidae) based on cytochrome *b* sequence variation. Journal of Mammalogy 75:321–327.

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.

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.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.

González, D., and A. P. Vovides. 2002. Low intralineage divergence in *Ceratozamia* (Zamiaceae) detected with nuclear ribosomal DNA ITS and chloroplast DNA *trnL-F* non-coding region. Systematic Botany 27:654–661.

Guerrero, J. A., E. De Luna, and C. Sánchez-Hernández. 2003. Morphometrics in the quantification of character state identity for the assessment of primary homology: an analysis of character variation of the genus *Artibeus* (Chiroptera: Phyllostomidae). Biological Journal of the Linnean Society 80:45–55.

Hall, E. R. 1981. The mammals of North America. Volume 1. 2nd ed. John Wiley & Sons, Inc., New York.

Handley, C. O. 1966. Descriptions of new bats (*Chiroderma* and *Artibeus*) from Mexico. Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología 36:297–301.

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

Hershkovitz, P. 1949. Mammals of northern Colombia, preliminary report no. 5: Bats (Chiroptera). Proceedings of the United States National Museum 99:429–454.

Huelsenbeck, J. P., B. Larget, R. E. Miller, and F. Ronquist. 2002. Potential applications and pitfalls of Bayesian inference of phylogeny. Systematic Biology 51:673–688.

Huelsenbeck, J. P., and F. Ronquist. 2001. MrBayes. Bayesian inference of phylogeny. Bioinformatics 17:754–755.

Irwin, D. M., T. D. Kocher, and A. C. Wilson. 1991. Evolution of the cytochrome *b* gene of mammals. Journal of Molecular Evolution 32:128–144.

Jones, J. K., Jr., and C. J. Phillips. 1970. Comments on the systematics and zoogeography of bats in the Lesser Antilles. Studies on the fauna of Curacao and other Caribbean islands 32:131–145.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16:111–120.

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

Koopman, K. 1993. Chiroptera. Pp. 137–241 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.

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

Maddison, D. R., and W. P. Maddison. 1992. MacClade version 3.04. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

Marcus, L. F. 1990. Traditional morphometrics. Pp. 77–122 in Proceedings of the Michigan morphometrics workshop (F. J. Rohlf and F. L. Bookstein, eds.). Special Publication, The University of Michigan Museum of Zoology 2.

Media Cybernetics. 1994. Image-Pro Plus version 1.0 for Windows. Media Cybernetics, Silver Spring, Maryland.

Mishler, B. D., and R. N. Brandon. 1987. Individuality, pluralism, and the phylogenetic species concept. Biology and Philosophy 2:397–414.

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.

Phillips, C. J., D. E. Pumo, H. H. Genoways, P. R. Ray, and C. A. Brishley. 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. and K. A. Crandall. 1998. ModelTest: testing the model of DNA substitution. Bioinformatics 14:817–818.

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., I. KIM, J. 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.

ROHLF, F. J. 1997. NTSYS-pc, version 2.01. Exeter Software, Setauket, New York.

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy: the principles and practice of numerical classification. W. H. Freeman and Company, San Francisco, California.

STATSOFT. 1998. Statistica 6.0 for Windows. StatSoft, Tulsa, Oklahoma.

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

TOLEDO, V. M. 1982. Pleistocene changes in vegetation in tropical Mexico. Pp. 93–111 in Biological diversification in the tropics (G. T. Prance, ed.). Columbia University Press, New York.

VAN DEN BUSSCHE, R., 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.

APPENDIX I

Taxa, geographic localities, and GenBank accession numbers of *Cytb* sequences of *Artibeus* specimens used for phylogenetic analysis. Numbers represent samples of *A. jamaicensis* plotted on Fig. 1.

Taxa	Locality	Accession Number
A. jamaicensis triomylus	Nayarit, Mexico (1)	AY144344
A. j. triomylus	Colima, Mexico (2)	AY144345
A. j. triomylus	Colima, Mexico (3)	AY382782
A. j. triomylus	Guerrero, Mexico (4)	AY114342
A. j. triomylus	Morelos, Mexico (5)	AY144346
A. j. yucatanicus	Veracruz, Mexico (6)	AY144340
A. j. yucatanicus	Oaxaca, Mexico (7)	AY144347
A. j. yucatanicus	Quintana Roo, Mexico (8)	AY144343
A. j. richardsoni	Chiapas, Mexico (9)	AY382785
A. j. richardsoni	Panama (10)	AY382784
A. j. richardsoni	Honduras (11)	AY382783
A. j. paulus	Chiapas, Mexico (12)	AY382786
A. j. jamaicensis	Puerto Rico (13)	NC002009[b]
A. hirsutus	Morelos, Mexico	AY144341
A. hirsutus	Sonora, Mexico	U66500[a]
A. inopinatus	Honduras	U66501[a]
A. lituratus	Morelos, Mexico	AY144338
A. lituratus	Veracruz, Mexico	AY144339
A. obscurus	Suriname	U66506[a]
A. obscurus	French Guiana	U66507[a]
A. planirostris fallax	French Guiana	U66503[a]
A. p. fallax	Suriname	U66504[a]
Dermanura azteca	Mexico	U66510[a]
D. tolteca	Panama	U66515[a]

[a] Sequences from Van Den Bussche et al., 1998.
[b] Sequence from Pumo et al., 1998.

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APPENDIX II

Specimens examined.—The 545 specimens included in morphometric analysis are listed below. Number of specimens, museum, or collectors are given in parentheses. Museum acronyms are as follow: IBUNAM, Colección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de México; ENCB, Colección de Mamíferos, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México; UAEM, Colección de Mamíferos de la Facultad de Ciencias Biológicas, Universidad Autónoma del Estado de Morelos, México; UAMI, Universidad Autónoma Metropolitana, Unidad Iztapalapa, México; CVULA, Colección de Vertebrados, Facultad de Ciencias, Universidad de Los Andes, Venezuela; ICN, Colección de Mamíferos, Instituto de Ciencias Naturales, Museo de Historia Natural, Colombia; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; FMNH, Field Museum of Natural History, Chicago, Illinois; TTU, Natural Science Research Laboratory, Texas Tech University, Lubbock, Texas; SNOMNH, The Sam Noble Muesum of Natural History, University of Oklahoma, Norman, Oklahoma. All specimens are from México, unless otherwise denoted.

Artibeus hirsutus.—Aguas Calientes: 5 km E Calvillo (2, ENCB 36991, 36992). Guerrero: Puente de Dios, 1 km N Yerbabuena (12, ENCB 39827–39830, 40072–40079). Estado de México: 1 km S Zacazonapan (1, ENCB 23355); 2 km S Zacazonapan (1, ENCB 23356); 1 km W Malinalco (1, ENCB 35250); 4 km N, 2 km W San Antonio del Rosario (1, ENCB 23366); 5 km N, 2 km W San Antonio del Rosario (1, ENCB 23369); 7 km N, 2 km E Zacualpan (1, ENCB 21623); Gruta La Estrella, 6 km S, 4 km E Tonatico (6, ENCB 22696–22698, 22700–22702); Ixtapan del Oro (4, ENCB 34822–34825). Michoacán: 13 km S, 7.5 km W Tepaliatepec (1, ENCB 26336); 19 km S, 6 km W Apatzingán (ENCB 24246, 24247); La Salada, 4 km S, 5 km E Zicuirán (7, ENCB 24251, 24252, 24255, 26342–26344, 26347; Santiago Conguripo, 12 km S, 21 km W Huetamo (3, ENCB 26426–26428).

Artibeus jamaicensis triomylus.—Colima: 1 km NW Ranchitos (18, SNOMNH 27169, 27182, 27184, 27185, 27198, 27205, 27225, 27215, 27217, 27240, 27242; IBUNAM 41490, 41476, 41473; uncataloged, MLRA 3085, 3126; uncataloged, TWH 333, 313). Guerrero: 1 km NW Playa Ventura, Copala (3, UAEM 124, 125, 130); Viveros El Huayacán, La Poza, Acapulco (5, IBUNAM 24843–24846, 34500); 2 km W Puerto Marquez, Acapulco (1, IBUNAM 24847); Planta agua Papagayo, La Sabana, Acapulco (1, IBUNAM 34506); Arroyo Seco, Acapulco (1, IBUNAM 34463); Agua de Obispo, 16.5 km N, 5 km E Tierra Colorada (5, ENCB 36574, 36576, 36583–36585); 2 km S, 0.25 km Tierra Colorada (7, ENCB 36586, 36587, 36591–36595). Jalisco: 3 km S El Grullo (6, ENCB 6725–6729, 6731); 1.5 km N, 5 km E Contla (2, ENCB 34942, 34959); 1.0 km SE Platanar (6, ENCB 34947–34949, 34963, 34972, 34982); 5.5 km NW San Marcos (1 ENCB, 29259); 1.5 km E San Sebastián (1, ENCB 34417); 2 km W San Sebastián (1, ENCB 34424); 2.5 km S, 5 km W San Sebastián (2, ENCB 34425, 34426); 2 km E Juanacatlán (1 ENCB, 34574). Estado de México: 9 km S Tejupilco (2, ENCB 21598, 21599); 10 km S, 2 km E de Tejupilco (6, ENCB 21600, 21601, 21603–21605, 21650); Santo Tomás de Los Platanos (8, ENCB 24838–24840, 24844–24848); Jalmolonga (4, ENCB 35244–35246, 35248). Michoacán (all specimens are uncataloged, but they will be deposited at IBUNAM): 1 km N Tuzantla (2, RHM 3; ANG 933); 1 km NW Caleta de Campos (1, AERM 369); 6 km NE Aquila, Los Tenamastos (4, ANG 323, 324, 332, 353); El Aguaje, 5 km N

Parícuaro (1, MLRA 2077); Apatzingán (1, MLRA 2381); Arroyo la Huacana (3, MLRA 2029–2031); Lago de Chandio, La Concha, 5 km W Apatzingán (2, MLRA 2331, 2371); Lajas del Bosque, Rancho Buena Vista (2, MLRA 2046, 2055); Río Chocola (1, BGM 35). Morelos: 1.5 km W La Nopalera, Yautepec (3, UAEM 20, 695, 696); 2 km S Yautepec (5, ENCB 24573–24576, 24578); Ejido El Limón, Tepalcingo (4, UAEM 196–198, 434); Huautla, Presa Cruz Pintada, Tlaquiltenango (4, UAEM 384, 399, 401, 487); Los Sauces, Tepalcingo (5, UAEM 200–203, 208). Nayarit: Punta Mita (1, UAEM 118); Isla La Peñita (4, UAEM 704, 705, 711, 716); Balneario El Nuevo Chapultepec, Jalcocotan (3, UAEM 724, 728, 729); 4 mi E San Blas (1, IBUNAM 29275). Puebla: 1 km NW Huehuetlán El Chico (1, UAMI 2620); 5 km SW Huehuetlán El Chico (5, UAMI 4156–4160); Huehuetlán El Grande (1, UAMI 9678); Teutla (5, UAMI 4168, 4169, 4171, 4174, 4175).

Artibeus jamaicensis yucatanicus.—Campeche: El Refugio Hopelchén, Hopelchén (1, IBUNAM 36619); Estación Centro de Ciencias del Mar, Ciudad del Carmen (1, IBUNAM 16592); 47 km NE Ciudad del Carmen (1, IBUNAM 30847); 27.5 km S Constitución, 70 km E Escárcega (2, IBUNAM 30848, 30849). Oaxaca: San Bartolomé Ayautla, Teatitlán de Flores Magón (10, IBUNAM 38030–38037, 38040, 38041); 2 km N Cuicatlán (12, ENCB 10885–10894, 10898, 10899). Puebla: Estación Vicente, Acatlán (4, IBUNAM 11425–11428); 10 km E, 5 km S Tuhuacán (9, UAMI 335–343); Villa Alegría, 6 km N Tehuacán (4, UAMI 8006–8009); 10 km N Tlacotepec de Díaz (4, UAMI 8024–8027). Quintana Roo: Playa Xpuhá, Playa del Carmen (3, UAEM 743–745); Xpuja, 25 km SW Playa del Carmen (8, ENCB 37270–37273, 37280, 37282, 37285, 37286); Ruinas de Kohunlich (2, IBUNAM 20150, 20152); Ruinas Tulum (3, IBUNAM 19074–19076); 2 km S, 7.5 km W Puerto Morelos (2, IBUNAM 31777, 31778); Ejido El Limonal, 15 km N San Pedro Peralta (3, IBUNAM 20148, 20149, 20245). San Luis Potosí: 2 km S de Taninul (20, ENCB 5937–5945, 5947–5950, 5952, 5954–5959); 29 km S, 5.5 km E Ciudad Valle (1, ENCB 18006); Cueva El Salitre, Xilitla (2, ENCB 33711, 33712). Tabasco (uncataloged): Ejido Jalapita, Huerta del Hotel Los Mangos, Centla (3, MLRA 3255, 3256, 3325); El Espino, Villahermosa (1, MLRA 3264). Tamaulipas: Cueva de Quintero, 2 km SSW Quintero (4, IBUNAM 2197, 8654–8656); Cueva del Abra, 12 km S Ciudad Mante (5, IBUNAM 8743, 8745, 8748, 8750, 8751). Veracruz: 3 km N Agua Dulce (2, MLRA 3274, 3275); La Mancha, 30 km N, 3 km E Cardel, Actopan (10, IBUNAM 26719–26723, 26713, 26714, 26727, 26729, 26730). Yucatán: 6 km S, 8 km W Las Coloradas (4, ENCB 34034–34037); 3.5 km S, 20 km E El Cuyo (2, ENCB 34100, 34103); 4 km S, 2 km W El Cuyo (8, ENCB 34055, 34057, 34058, 34105, 34106, 34108–34110); Río Lagartos (1, UAEM 740).

Artibeus jamaicensis paulus.—Chiapas: 5.5 km N, 17.6 km W Ocozocuautla (15, ENCB 13020–13034); 13.5 km E de Chiapa de Corzo (2, ENCB 5497 5498); 7.6 km S, 5.7 km E Revolución Mexicana (3, ENCB 18608–18610); 9 km N, 13.6 km E Pijijiapan (6, ENCB 18616, 18617, 18619, 18621–18623); 6.4 km S, 3.1 km E Jaltenango (4, ENCB 18611–18614). EL SALVADOR: Ahuachapan, Barra de Santiago (1, MVZ 130866). La Union, Tabanco, Rosalia Mine (3, MVZ 130867, 130868, 130870). Morazan, about 0.5 miles (0.8 km) N Monte Mayor, Tempisque Mine (7, MVZ 130873–130879). GUATEMALA: Alta Verapaz, Lanquin, Cave of Lanquin (1, FMNH, 64474). Escuintla (3, FMNH 64948, 64949 64955); Escuintla, Finca El Zapote (2 FMNH 64479, 64636). Alta Verapaz (1, FMNH 64953). Izabal, Escobas (3, FMNH 41932–41934).

Artibeus jamaicensis richardsoni.—Chiapas: Estación Chajul, Reserva de Montes Azules (9, IBUNAM 22277–22279, 22288, 22289, 22298, 22933, 22932, 24431); Arroyo José, Reserva de Montes Azules, Ocosingo (4, IBUNAM 22299–22301, 22840); Ejido Benemérito de las Américas, Ocosingo (5, IBUNAM 20334, 20310–20312, 20330); Ejido la Gloria, Río Lagartos, Ocosingo (1, IBUNAM 19257). PANAMA: Darien; Yaviza (1, MVZ 135977); Parque Nacional Darien, Rancho Frío (5, MVZ 128111–128115). Limón; 4.6 km W Puerto Limon (2, MVZ 164782, 164785). Panama Bay (3, MVZ 19206–19208). COSTA RICA: Villa Quesada (1, FMNH, 43977). Guanacaste; 2 km S, 12 km E Bolson (3 FMNH 123130–123132). HONDURAS: Tapasuna (1, MVZ 47635). Atlantida; Lancetilla Botanical Garden (1, TTU 84180).

Artibeus jamaicensis jamaicensis.—COLOMBIA: Isla Providencia; Smooth Water Bay (9, ICN 1103–1108, 1119, 1126, 6569); Bottom House, Big Gulley (4, ICN 6523, 6527, 6567, 6571); Kalaco Point, Aguamansa (1, ICN 6541); Fresh Water Creek (2, ICN 6566, 6568). San Andrés; Isla Fragasa (9, ICN 1300, 1301, 1303, 1305, 1306, 1323, 1337, 6537, 6533). DOMINICAN REPUBLIC: Santo Domingo; northern suburb (2, FMNH 108323, 108327). HAITI: Port au Prince, Diquini cave (1, FMNH 30776). JAMAICA: St. Ann, 4 miles (6.5 km) E Runaway Bay (6, TTU 21793–21798).

Artibeus lituratus.—Chiapas: 1.5 km N, 8 km W Ocozocoautla (2, ENCB 13035, 13036); 9 km N, 8 km E Ocozocuautla (1, ENCB 13037); Cañón del Sumidero, 4 km N, 5.3 km W Tuxtla Gutiérrez (4, ENCB, 15512, 15513, 15515, 15521). Guerrero: 1 km N, 3.5 km E Petacalco (9, ENCB 35488, 35490, 35491, 35493, 35495, 35496, 35502, 35588, 35589). Morelos: 2 km E Oaxtepec (3, ENCB 35700, 24609, 24610); 2.5 km N, 2.7 km E Yautepec (1, ENCB 21056); 3 km S Yautepec (1, ENCB 24611); 3.5 km N, 2.8 km E Cuautla (2, ENCB 21082, 24606); Tetela del Volcán (2, ENCB 21080, 21081). Puebla; 1 km S Piaxtla (4, ENCB 28515, 28509, 28522, 28523); 3 km NW Metlaltoyuca (2, ENCB 27971, 27972); 4 km NW Atlixco (2, ENCB 28512, 28514); Chietla (1, ENCB 15155). Tabasco: 7 km N Teapa (4, ENCB 13856–13859); Cocona, 2 km E Teapa (2, ENCB 13855, 13864); Rancho Santo Tomás, 1 km S Teapa (2, ENCB 41111, 41112). Veracruz: 1 km E Teocelo (1, ENCB 4651); 11 km NE Catemaco (2, ENCB 1786, 1787); 2 km SW San Juan Evangelista (2, ENCB 15138, 15139); 4 km N, 7.5 km W Actopan (3, ENCB 16216, 16217, 16226); Cuitlahuac (2, ENCB 15885, 15887).

Artibeus obscurus.—VENEZUELA: Bolivar; Salto el Jaspe (La Gran Sabana) near Dal Rafael de Mapauri (1, CVULA 828); Las Piñas, La Paragua (3, CVULA 1728, 1733, 1734); Reserva Forestal de Imataca, 30 km E Tumeremo (2, CVULA 3416, 3417). COLOMBIA: Meta; San Juan de Arama, parte N de la Serranía La Macarena, Caño La Curia (7, ICN 10562, 10563, 10566, 10572, 10573, 10581, 10584). Vichada; PNN, El Tuparro, alrededores del Centro Administrativo (1, ICN 12693). Amazonas; Leticia, km 7 vía Tarapacá (2, ICN 14904, 14910). ECUADOR: Napo; Laguna Grande, Río Cuyabeno, 00° 00′ N, 176°11′ W (1, FMNH 124858); Río Aguarico, 200 m SW of mouth of Rio Cuyabeno (5, FMNH 124861–124865). PERU: Loreto; Alto Amazonas, Río Morona, Quebrada Pashaga (4, FMNH 89070–89073). Huanuco; Agua Caliente, Río Pachitea (3, FMNH 55393, 55397, 55398).

Artibeus planirostris fallax.—VENEZUELA: Bolivar; La Paragua (6, CVULA 1690, 1713, 1714, 1717, 1719, 1763). COLOMBIA: Meta; Restrepo, 1 km E sede de la Universidad del Llano, Finca La Esperanza (4, ICN 14362, 14363, 14365, 14366); Restrepo, Caney Alto, Rio Caney (1, ICN 14367); Caney Alto (1, ICN 11387); Puerto López, Vereda Manegua Bajo, Finca El Lagunazo (1, ICN 14112); Restrepo, near Universidad Del Llano (1, ICN 14361); San Juan de Arama, parte N de la Serranía La Macarena, Caño La Curia (6, ICN 10637, 10641, 10644–10647). FRENCH GUIANA: Cayenne (1, FMNH 14886). SURINAM: Kaiserberg, airstrip, Zuid River (5, FMNH 93198–93202). BRAZIL: Para; Rio Tapajoz, E Fordlandia (2, FMNH 92067, 92069); Rio Amazonas, Ilha do Urucurituba (1, FMNH 92073); Santarem, Río Amazonas (1, FMNH 66205).