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Taxonomic status of Andersen's fruit-eating bat (*Artibeus jamaicensis aequatorialis*) and revised classification of *Artibeus* (Chiroptera: Phyllostomidae)

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Abstract

Fruit-eating bats of the genus *Artibeus* are widely distributed across the Neotropics and are one of the most recently evolved assemblages of the family Phyllostomidae. Although the taxonomy and systematics of species of *Artibeus* has been the subject of an intense historical debate, the most current taxonomic arrangements recognize approximately eleven species within the genus. However, recent phylogenetic studies indicate that species diversity within South and Middle American populations of *Artibeus* is underestimated. South American populations referable to *A. jamaicensis aequatorialis* are of considerable interest because previous studies of mitochondrial DNA variation identified potential species level variation west of the Andes Mountains. In this study we use morphometric and genetic data (nuclear AFLPs) to investigate the taxonomic status of *A. j. aequatorialis*. Our results indicate that elevating *aequatorialis* to species level is appropriate based on statistically supported reciprocal monophyly in mitochondrial and nuclear datasets and diagnostic morphological characters. In light of our results, and of those presented elsewhere, we provide a revised classification of the genus.

Key words: AFLPs, allopatric speciation, Neotropical bats, Ecuador, systematics

Resumen

Los murciélagos frugívoros del género *Artibeus* están ampliamente distribuidos en el Neotrópico y son uno de los ensamblajes más recientemente evolucionados de la familia Phyllostomidae. Aunque la taxonomía y sistemática de las especies de *Artibeus* ha sido objeto de un intenso debate histórico la clasificación taxonómica más reciente reconoce aproximadamente once especies dentro del género. Sin embargo, estudios filogenéticos recientes muestran que la diversidad de especies en las poblaciones de Sur y Central América está subestimada. Las poblaciones sudamericanas de *A. jamaicensis aequatorialis* son de considerable interés dado que estudios previos usando ADN mitocondrial identificaron una potencial variación a nivel de especie en las poblaciones distribuidas al occidente de los Andes. En el presente estudio nosotros usamos datos morfométricos y genéticos (AFLPs nucleares) para evaluar el estado taxonómico de *A. j. aequatorialis*. Nuestros resultados indican que elevar *aequatorialis* al estatus específico es apropiado dada la monofilia recíproca, estadísticamente soportada por datos mitocondriales y nucleares y la existencia de caractéres morfológicos diagnósticos. A la luz de nuestros resultados, y de otros presentados previamente, nosotros proveemos una revisión de la clasificación del género.

Palabras clave: AFLPs, especiación alopátrica, murciélagos Neotropicales, Ecuador, sistemática

Introduction

Bats of the genus *Artibeus* Leach 1821 are an important component of the Neotropical chiropteran fauna and comprise a diverse and recent radiation of the family Phyllostomidae (Baker *et al.* 2003; Baker *et al.* in press). The taxonomic history of the genus is complex, with some authors considering the genus to be a polytypic assemblage including the subgenera *Dermanura* Gervais and *Koopmania* Owen and others considering

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Dermanura and *Koopmania* as distinct genera (for a brief review see Marques-Aguiar 2008). However, a large amount of data support the hypothesis that *Artibeus* (*sensu stricto*) represents a monophyletic assemblage of bats and is as distinct from *Dermanura* as are many other genera in the subfamily Stenodermatinae (Van Den Bussche *et al.* 1998; Hoofer *et al.* 2008; Solari *et al.* 2009). Herein, we follow the classification of Hoofer *et al.* (2008) and regard *Artibeus* as monophyletic, with *Dermanura* representing a distinct genus and *Koopmania concolor* included within *Artibeus*. Following this taxonomic arrangement, eleven species of *Artibeus* are recognized: *A. amplus* Handley, *A. concolor* Peters, *A. fimbriatus* Gray, *A. fraterculus* Anthony, *A. hirsutus* Andersen, *A. inopinatus* Davis and Carter, *A. jamaicensis* Leach, *A. lituratus* Olfers, *A. obscurus* Schinz, *A. planirostris* Spix, and *A. schwartzi* Jones.

Although the systematics and taxonomy of species of *Artibeus* have been investigated by a number of authors (Andersen 1906; Andersen 1908; Davis 1984; Handley 1987; Marques-Aguiar 1994; Lim 1997; Van Den Bussche *et al.* 1998; Guerrero *et al.* 2004; Lim *et al.* 2004; Larsen *et al.* 2007; Guerrero *et al.* 2008; Hoofer *et al.* 2008; Redondo *et al.* 2008; Larsen *et al.* 2010), the potential for unrecognized species level variation within the genus remains (Guerrero *et al.* 2004; Larsen *et al.* 2007; Redondo *et al.* 2008). For example, using mitochondrial DNA sequence data, Redondo *et al.* (2008) identified possible species level diversity within Brazilian populations traditionally recognized as *A. obscurus*. Furthermore, recent phylogenetic analyses of the genus have altered the species boundaries and associated geographic distributions of several forms (Larsen *et al.* 2007). Among the most significant alterations is the recognition of *A. planirostris* as a species (including the subspecies *fallax*, *grenadensis*, *hercules*, and *trinitatus*) distinct from the *A. jamaicensis* complex, which thereby restricts the known South American distribution of *A. jamaicensis* to west of the Andes Mountains (Larsen *et al.* 2007). South American representatives of the *Artibeus jamaicensis* complex are of particular interest because populations referable to *A. jamaicensis aequatorialis* distributed west of the Andes Mountains in northern Peru, Ecuador, and Colombia may warrant species level status. Indeed, previous phylogenetic analyses of mitochondrial DNA sequence variation indicate a sister relationship between *aequatorialis* and the remainder of the *A. jamaicensis* subspecies (Larsen *et al*. 2007, Hoofer *et al*. 2008).

The objective of the current analysis is to investigate the taxonomic status and evolutionary history of *A. jamaicensis aequatorialis*. Specifically, we test the hypothesis of the species level status of *aequatorialis* by examining congruence among multiple datasets (see Baker and Bradley 2006; Baker et al. 2009).
To accomplish this we analyze nuclear Amplified Fragment Length Polymorphisms (AFLPs), which are ideally suited for elucidating species boundaries within *Artibeus* (Larsen *et al*. 2010), and morphological data generated from individuals of *A. jamaicensis aequatorialis* collected throughout western Ecuador, including specimens from near the type locality (Zaruma, Ecuador; Andersen 1906). We examine our results with respect to levels of interspecifc variation observed across these datasets. In light of our conclusions, we evaluate the specific status and phylogenetic relationships of species within *Artibeus* and provide a classification of all known extant species that establishes monophyly.

Material and methods

Morphometric methods. One-hundred thirty four specimens (see Appendix I) were examined from six subspecies of *Artibeus jamaicensis* (*A. j. aequatorialis*, n = 79, ♀ = 42 and ♂ = 37; *A. j. jamaicensis*, n = 16, ♀ = 12 and ♂ = 4; *A. j. parvipes*, n = 3, ♀ = 3; *A. j. paulus*, n = 7, ♀ = 5 and ♂ = 2; *A. j. richardsoni*, n = 22, ♀ = 12 and ♂ = 10; and *A. j. yucatanicus*, n = 7, ♀ = 1 and ♂ = 6). Additionally, 43 individuals of two congeneric sympatric species of *A. j. aequatorialis* (*A. fraterculus*, n = 27, ♀ = 16 and ♂ = 11; and *A. lituratus*, n = 16, ♀ = 7 and ♂ = 9) were included for comparisons. The material analyzed includes dry (skull, skins) and fluid-preserved specimens. Specimens examined were deposited in the following natural history collections: American Museum of Natural History, New York (AMNH), Museo de la Escuela Politécnica Nacional del Ecuador , Quito (MEPN); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ); Natural Science Research Laboratory of the Museum of Texas Tech University, Lubbock (NSRL; TTU =

voucher number, TK = tissue number); Texas Cooperative Wildlife Collection, College Station (TCWC); and the United States National Museum, Washington, D.C. (USNM).

We used 14 cranial and mandibular measurements to assess the phenetic variation among subspecies of *A. jamaicensis* (*sensu* Larsen *et al.* 2007) and to assess interspecific comparisons with respect to *A. fraterculus* and *A. lituratus*. Measurements were taken to the nearest 0.01 mm with a digital caliper. Only adult specimens (based on the degree of fusion of skull sutures and epiphysis of wing phalanges [Anthony 1988]) were included in our analyses. Males and females were not combined because previous analyses identified sexual dimorphism in populations of *A. j. aequatorialis* (Marchán-Rivadeneira 2006). Measurements taken included: greatest skull length (GSL); condyloincisive length (CIL); height of skull (SH); mastoidal breadth (MB); greatest width of braincase (BRW); zygomatic arch breadth (ZB); postorbital constriction width (POW); breadth across upper canines (C1C1); breadth across the outer edges of the second upper molars (M2M2); palatal length (PL); maxillary toothrow length (MXTR); mandible length (ML); length of mandibular toothrow (MLT); and breadth across lower canines (c1c1). These measurements have been widely used to analyze the morphometric variation in *Artibeus* (Patten 1971; Marques-Aguiar 1994; Lim 1997; Marchán-Rivadeneira 2006).

All measurements were transformed to their natural logarithms to correct for deviations from the assumptions of normality and homoscedasticity (Sneath & Sokal 1973; Sokal & Rohlf 1995; Zar 1998), and to make the variance independent from the magnitude of each measurement (Schnell 1970). We performed a principal component analysis (PCA) to summarize the morphometric variation contained in a covariance matrix and to explore intraspecific morphological variation within the *Artibeus jamaicensis* complex. Euclidian distances were calculated based on mean values to assess overall morphological similarity. Analyses were conducted using SPSS (version 13.0) and Matlab (version 6.5), and were performed using 1000 iterations.

Molecular methods. Thirty-nine individuals from six species of *Artibeus* (including 7 individuals of *A. jamaicensis aequatorialis*) were genotyped using AFLP bands. Vouchers for all genotyped specimens were morphologically identified and were also molecularly identified with mtDNA (cytochrome-*b*) sequence data (Larsen *et al.* 2007; Hoofer *et al.* 2008; Larsen *et al.* 2010). Tissue and museum voucher numbers for all specimens examined are listed in Appendix I.

AFLP methods followed Vos *et al.* (1995), Phillips *et al.* (2007), and McDonough *et al.* (2008) with slight modifications. Specifically, our AseI adapter sequences were as follows: 5'-GAC-GAT-GAG-TCC-TGA-G-3' and 5'-TAC-TCA-GGA-CTC-AT-3'. Genotyping was performed using an ABI 3100-*Avant* genetic analyzer (Applied Biosystems, Foster City, California). AFLP fragments were scored for presence or absence using GeneMapper v. 4.0 software (Applied Biosystems). AFLP profiles were anonymously double read, and only fragments (50-400bp in length) with intensity larger than 100 RFUs were selected using GeneMapper version 4.0 software (Applied Biosystems). A binary data matrix was created using GenAlEx version 6 software (Peakall & Smouse 2006). Initially 15 primer combinations were examined, of which 6 primer pairs (*ECO* RI + 3 bases; *ASE* I + 3 bases) produced distinct scorable fragments within a 400bp region (for primer sequences see McDonough *et al.* 2008).

Genetic analyses. The binary AFLP dataset was analyzed using MrBayes, version 3.1 (Huelsenbeck & Ronquist 2001), PAUP* version 4.0b10 (Swofford 2002), and GenAlEx version 6 (Peakall & Smouse 2006) software packages. An analysis of molecular variance (AMOVA; Excoffier *et al.* 1992) was performed to examine significance of genetic variation among and within species using GenAlEx software. Neighbor-joining, maximum-parsimony, and Bayesian analyses were used to identify structure in the AFLP dataset. Maximum parsimony (unweighted Wagner) was performed using heuristic searches, 500 replicates of the random taxon addition option, each with random starting trees, and tree-bisection-reconnection branch swapping. For bootstrap support values, 500 replicates were conducted using the heuristic search criterion. Posterior probabilities were generated using the binary evolutionary model as implemented within Mr. Bayes software. Bayesian analyses were performed with 4 Monte Carlo chains using 1 million generations with a burn-in value of 1,000 trees. Genetic distances using the Nei-Li model were generated in PAUP* software.

Results

Morphological analyses. Within *A. jamaicensis* the mean values for females and males of nearly all cranial and mandibular measurements were larger for *A. j. aequatorialis* (Appendix II). In addition, interspecific mean differences among *A. j. aequatorialis*, *A. fraterculus*, and *A. lituratus* showed intermediate values for *A. j. aequatorialis*. However, the postorbital constriction width (POW) was larger in *A. j. aequatorialis* with respect to *A. lituratus*. Morphological variation examined by PCAs showed that loadings of the first principal component (PC1) for the skull measurements in females and males were all high, positive and relatively uniform, indicating mainly skull size variation (Table 1). Along PC1, 70.71% of the total variation was accounted by females and 72.10% by males. PC2 accounted for 8.23% and 6.48% (females and males, respectively) of the variation in the sample and was interpreted as variation in shape. For females and males, the POW measurement was high and positively correlated with PC2, suggesting that this factor primarily represents shape variation in the orbital constriction. In the PCA, the variation within *A. jamaicensis* showed overlap along PC1 and PC2 (Fig. 1A–B). Along PC1, skull size variation among subspecies of *A. jamaicensis* ranged from *A. j. parvipes* being the smallest to *A. j. aequatorialis* being the largest. Euclidian distances showed that *A. j. richardsoni* is morphologically more similar to *A. j. aequatorialis* (Table 2).

TABLE 1. Results of the principal component analysis (PCA) for females and males of *Artibeus jamaicensis aequatorialis, A. j. jamaicensis, A. j. parvipes, A. j. paulus, A. j. richardsoni*, and *A. j. yucatanicus* (n = 134) based on 14 cranial and mandibular measurements. Only loadings of the first tree principal components (PC) are presented because together they accounted for more than the 80% of the variance in the sample. Variables are defined in Materials and Methods.

	Component					
	Females			Males		
Variable	PC1	PC2	PC3	PC1	PC2	PC3
GSL	0.94	0.09	-0.07	0.92	-0.01	0.18
CIL	0.92	0.01	-0.14	0.93	-0.10	0.20
SH	0.70	0.40	-0.03	0.77	0.40	0.02
MB	0.74	0.35	-0.11	0.85	0.22	0.23
BRW	0.75	0.42	-0.17	0.78	0.28	0.13
ZB	0.86	0.25	-0.04	0.81	0.26	0.15
POW	0.18	0.60	0.75	0.04	0.87	-0.06
C1C1	0.90	-0.27	0.04	0.88	-0.02	-0.34
M2M2	0.92	0.07	0.02	0.91	0.05	-0.07
PL	0.91	0.07	-0.10	0.87	-0.14	0.28
MXTR	0.88	-0.01	0.02	0.92	-0.12	0.02
ML	0.91	-0.05	-0.14	0.92	-0.14	0.23
MLT	0.90	0.03	-0.08	0.91	-0.13	0.05
c1c1	0.80	-0.46	0.30	0.81	-0.07	-0.51
% Variance	70.71	8.23	5.18	72.10	6.48	6.30

AFLPs. Six primer pairs (*ECO* RI + 3 bases; *ASE* I + 3 bases) used for selective amplification produced 414 scorable bands. Of the 414 scored bands, 108 were monomorphically present in all specimens examined and 306 were polymorphic (with 211 being parsimony informative). The average interspecific Nei-Li genetic distance value across the species examined was 3.7%, ranging from 4.5% (*A. inopinatus* vs. *A. fraterculus*) to 2.7% (*A. j. aequatorialis* vs. *A. planirostris*) (Table 3). All phylogenetic analyses revealed 7 statistically supported clades, corresponding to the 6 species used in our analyses, plus an additional clade corresponding to populations of *A. jamaicensis aequatorialis* west of the Andes Mountains in Ecuador (Fig. 2). Additionally, the AMOVA indicated significant genetic structure (PhiPT = 0.42; $P < 0.001$) among the 7 clades, with 42% of the total genetic diversity residing among species (including *aequatorialis*) and 58% within species.

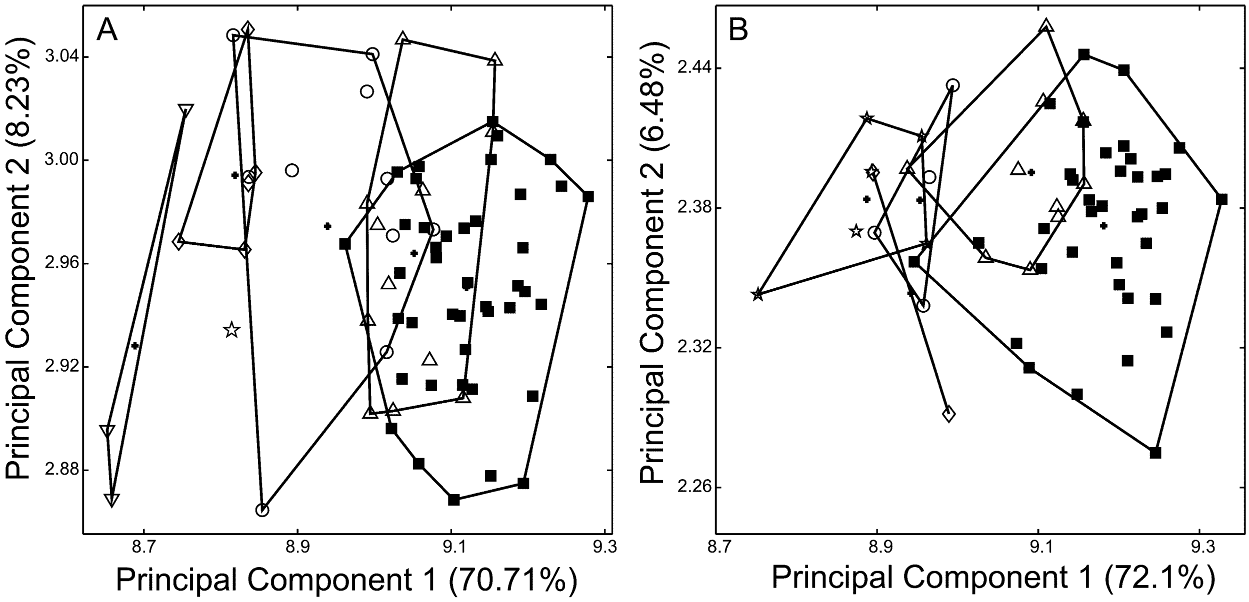

FIGURE 1. Scatter plots of the first and second principal component scores of a Principal Components Analysis for females (A) and males (B) based on 14 cranial and mandibular measurements for 6 traditionally recognized subspecies of *Artibeus jamaicensis* (■ = *aequatorialis*; ○ = *jamaicensis*; ▽ = *parvipes*; ◊ = *paulus*; Δ = *richardsoni*; ☆ = *yucatanicus*).

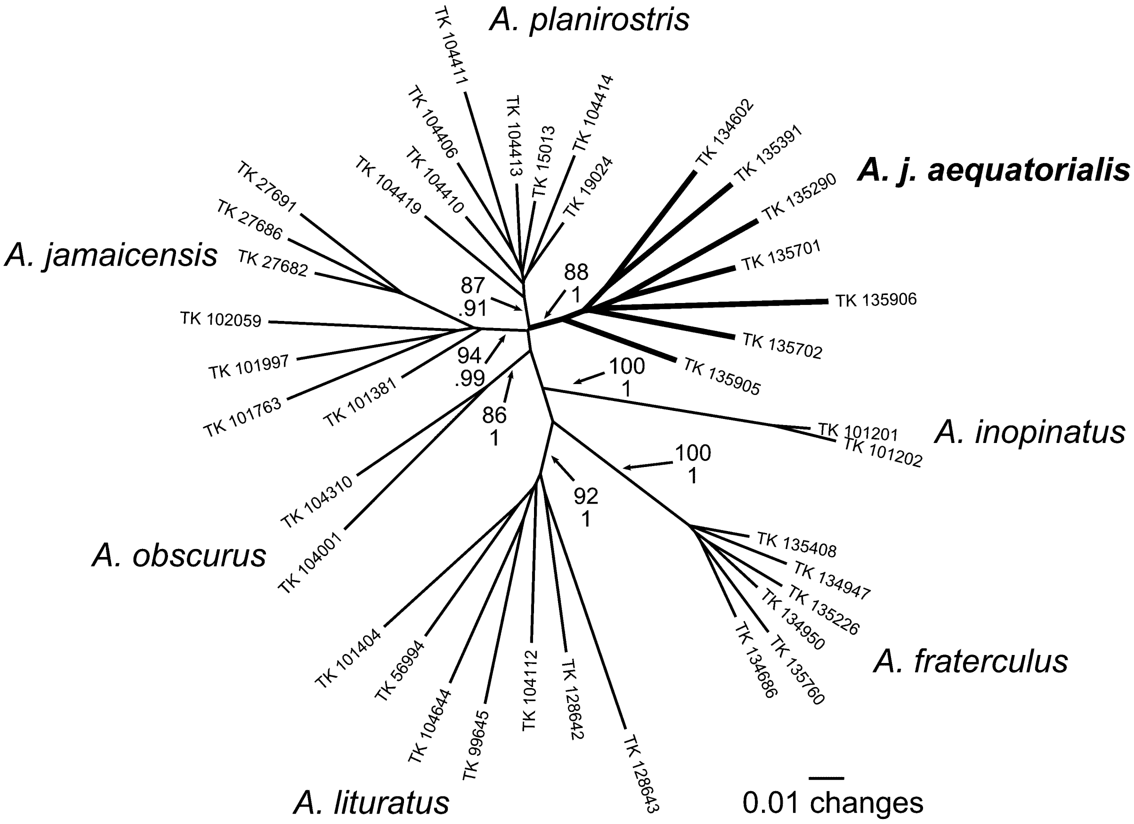

FIGURE 2. Unrooted neighbor-joining phylogram based on 414 AFLP bands. Numbers along branches indicate bootstrap support values (top score) and Bayesian posterior probabilities (bottom score). Bold clade identifies specimens traditionally recognized as *Artibeus jamaicensis aequatorialis*.

TABLE 2. Morphological similarity using euclidian distances calculated on mean values based on 14 cranial and mandibular measurements of traditionally recognized subspecies (females and males separated) of *Artibeus jamaicensis*.

	Euclidian Distances: Females					
	1	2	3	4	5	6
1) *A. j. aequatorialis*						
2) *A. j. jamaicensis*	0.28					
3) *A. j. parvipes*	0.28	0.20				
4) *A. j. paulus*	0.28	0.15	0.20			
5) *A. j. richardsoni*	0.08	0.28	0.28	0.28		
6) *A. j. yucatanicus*	0.28	0.15	0.20	0.10	0.28	

	Euclidian Distances: Males				
	1	2	3	4	5
1) *A. j. aequatorialis*					
2) *A. j. jamaicensis*	0.22				
3) *A. j. paulus*	0.22	0.08			
4) *A. j. richardsoni*	0.10	0.22	0.22		
5) *A. j. yucatanicus*	0.22	0.09	0.09	0.22	

TABLE 3. Nei-Li genetic distances (percent values) based on 414 AFLP bands from *Artibeus jamaicensis aequatorialis* and six species of *Artibeus*.

	1	2	3	4	5	6	7
1) *A. j. aequatorialis* (n = 7)							
2) *A. fraterculus* (n = 6)	4.3						
3) *A. inopinatus* (n = 2)	4.1	4.5					
4) *A. jamaicensis* (n = 7)	3.2	4.2	4.3				
5) *A. lituratus* (n = 7)	4.0	3.7	4.2	4.1			
6) *A. obscurus* (n = 2)	3.3	3.8	4.3	3.2	3.9		
7) *A. planirostris* (n = 8)	2.7	3.9	3.7	2.8	3.6	2.8	

Discussion

Our nuclear AFLP data, in combination with the mtDNA sequence data previously reported (Larsen *et al.* 2007; Hoofer *et al.* 2008), indicate that the traditionally recognized subspecies *A. jamaicensis aequatorialis* forms a monophyletic assemblage separate from the remainder of the *A. jamaicensis* complex. Previously, Larsen *et al.* (2007) phylogenetically analyzed cytochrome-*b* gene sequence data from specimens of *A. jamaicensis aequatorialis* collected west of the Andes Mountains in Ecuador. Their data showed that *A. j. aequatorialis* formed a statistically supported sister clade relative to the remaining Central American and Caribbean subspecies of *A. jamaicensis*, and that *aequatorialis* is separated from those subspecies by a genetic distance of ~4.4%. It is important to note that this genetic distance value is similar to (or greater than) the interspecific genetic distance values that define several Stenodermatine species (e.g. *Dermanura tolteca* versus *D. phaeotis*: Solari *et al.* 2009; and species of *Platyrrhinus*: Velazco and Patterson 2008). The data presented herein provide further evidence that populations of *A. j. aequatorialis* distributed west of the Andes are isolated from the remainder of the *jamaicensis* complex. The nuclear AFLP data from *A. j. aequatorialis* (including specimens from the type locality of Zaruma, Ecuador; Andersen 1906) form a statistically supported clade separate from Central American and Caribbean subspecies (Fig. 2). *Artibeus jamaicensis* *aequatorialis* is defined in our AFLP data by 15 unique bands and is separated from Central American and Caribbean *A. jamaicensis* by a Nei-Li genetic distance value of 3.75%, values that are comparable to those for other species in the genus (Table 3). Based on statistically supported reciprocal monophyly in mitochondrial and nuclear datasets and diagnostic morphological characters, we recognize *aequatorialis* as a species distinct from *A. jamaicensis*. Justification for recognition of *A. aequatorialis* is the Genetic Species Concept (*sensu* Baker and Bradley 2006) using the criterion of statistically supported monophyly in multiple datasets (see Baker *et al.* 2009). Recognition of *A. aequatorialis* reinforces previous hypotheses that *A. jamaicensis* may be entirely absent from South America, or if present, restricted to northern Colombia or the Caribbean coasts of Colombia and Venezuela (Larsen *et al.* 2007; Redondo *et al.* 2008).

We hypothesize that the origin of *A. aequatorialis* is compatible with an allopatric model of speciation by the Bateson-Dobzhansky-Muller (BDM) process (Baker & Bradley 2006). Evidence for this hypothesis comes from the phylogeographic structuring observed within the lineage giving rise to *Artibeus aequatorialis* and the remainder of *A. jamaicensis* complex (see mtDNA data presented in Larsen *et al*. 2007), which suggests sustained periods of isolation west of the Andes Mountains in South America (*A. aequatorialis*) and throughout Central America (e.g. *A. j. richardsoni* and *A. j. triomylus*). Furthermore, relaxed molecular clock analyses presented in Larsen *et al.* (2010) indicate the time to the most recent common ancestor (TMRCA) for the lineages distributed west of the Andes Mountains and Central America (*A. aequatorialis* and *A. jamaicensis*) and those with origins east of the Andes (e.g. *A. obscurus*, *A. lituratus*, and *A. planirostris*) is approximately 2.5 million years (MY) (±0.6 MY). This value is consistent with recent uplifts of the Andes (5 MY to present; Gregory-Wodzicki 2000) and formation of suitable habitat along the coastal lowlands of Ecuador and Colombia (Mégard 1992; Nores 2004). The TMRCA for *A. aequatorialis* and *A. jamaicensis* was estimated at approximately 1.5 MY (±0.5 MY; Larsen *et al.* 2010), which is consistent with isolation resulting from sea level fluctuations and associated habitat fragmentation of the northern regions west of the Andes during the Pleistocene (Nores 2004). Noticeably, the patterns of endemism present in species of *Artibeus* along the western slope of the Andes northward to Central America (see Patterson *et al.* 1992 and Hoofer *et al.* 2008) are comparable to those in several other taxonomic groups (e.g. Haffer 1967; Brown 1975; Prance 1982; Rheindt *et al.* 2009).

Revised classification of *Artibeus*. Our results and those of Larsen *et al.* (2007), Larsen *et al.* (2010), and Redondo *et al.* (2008), indicate that there are at least 12 species that comprise the genus *Artibeus* (Table 4). Additional species level variation may exist in at least three species, *A. jamaicensis*, *A. lituratus*, and *A. obscurus*; and thus detailed taxonomic studies of these are warranted. Specifically, Panamanian populations referred to as *A. jamaicensis richardsoni* and Mexican populations of *A. j. triomylus* may be genetically isolated from the remaining subspecies of *A. jamaicensis* (see Larsen *et al.* 2007 and Guerrero *et al.* 2004); and the debate regarding the subspecific/specific status of *intermedius* in Central American populations traditionally referred to as *A. lituratus* requires additional genetic analyses of data from the nuclear genome. Redondo *et al.* (2008) identified potential species level variation in populations historically identified as *A. obscurus* in southeastern Brazil and Venezuela. These populations may represent an unnamed taxon, inasmuch as *Artibeus obscurus* is considered to be monotypic. As noted by Redondo *et al*. (2008), *Artibeus fuliginosus* Gray 1838 is available for *A. obscurus* "like" forms distributed east of the Andes Mountains. Unfortunately, a detailed morphological comparison with the holotype of *A. fuliginosus* may be impossible as Handley (1989) indicated that the specimen was missing and presumably lost.

Species account

Artibeus aequatorialis Andersen, 1906

Andersen's Fruit-eating Bat

Artibeus jamaicensis aequatorialis Andersen, 1906
Artibeus jamaicensis aequatorialis Andersen, 1908
A[*rtibeus*]. *l*[*ituratus*]. *aequatorialis*: Hershkovitz, 1949: 447; name combination.

Holotype. BMNH 0.2.9.13: adult male, skin and skull; collected by Perry O. Simons, no. 395, 17 June 1899.

Type locality. Ecuador: Department of El Oro, Zaruma; 1000m.

Distribution. West of the Andes Mountains from northern Peru, northward throughout western Ecuador to Colombia (Fig. 3). The northernmost and southernmost distribution of *A. aequatorialis* in Colombia and Peru, respectively, is unknown. Elevation ranges from 22m (Ecuador: Guayas) to 1,106m (Ecuador: El Oro). This species seems to exploit a variety of habitats, ranging from the dry forests of northern Peru and southern Ecuador to the tropical forests of the Chocó in Colombia. Occurs sympatrically with *Artibeus fraterculus* and/or *A. lituratus* throughout most of its distribution.

TABLE 4. Revised classification of *Artibeus*. Asterisk indicates *A. schwartzi* may be of hybrid origin (Larsen *et al.* 2010). *Artibeus jamaicensis, A. lituratus,* and *A. obscurus* are in bold, indicating potential unrecognized species diversity within Mexican, Central American, and Brazilian populations, respectively (see Guerrero *et al.* 2004, Davis 1984, and Redondo *et al.* 2008). Note: Simmons (2005) incorrectly cited Allen (1897) for the description of *palmarum*. The original description of *palmarum* was by Allen and Chapman (1897).

- Genus *Artibeus* Leach, 1821
  - *Artibeus aequatorialis* Andersen, 1906
  - *A. amplus* Handley, 1987
  - *A. concolor* Peters, 1865
  - *A. fimbriatus* Gray, 1838
  - *A. fraterculus* Anthony, 1924
  - *A. hirsutus* Andersen, 1906
  - *A. inopinatus* Davis and Carter, 1964
  - ***A. jamaicensis*** Leach, 1821
    - *A. j. jamaicensis* Leach, 1821
    - *A. j. parvipes* Rehn, 1902
    - *A. j. paulus* Davis, 1970
    - *A. j. richardsoni* Allen, 1908
    - *A. j. triomylus* Handley, 1966
    - *A. j. yucatanicus* Andersen, 1908
  - ***A. lituratus*** (Olfers, 1818)
    - *A. l. intermedius* Allen, 1897
    - *A. l. koopmani* Wilson, 1991
    - *A. l. lituratus* Olfers, 1818
    - *A. l. palmarum* Allen and Chapman, 1897
  - ***A. obscurus*** (Schinz, 1821)
  - *A. planirostris* Spix, 1823
    - *A. p. fallax* Peters, 1865
    - *A. p. grenadensis* Andersen, 1906
    - *A. p. hercules* Rehn, 1902
    - *A. p. trinitatus* Andersen, 1906
  - *A. schwartzi** Jones, 1978

Specimens examined. (n = 79) (* indicates specimen used in molecular analyses). Ecuador: Azuay, Manta Real Manglar (2°33'60"S, 79°21'20"W), 1 ♀ (MEPN 913072); Bolivar, Barraganate (1°27'20"S, 79°19'60"W), 1 ♂, 1 ♀ (MEPN 80412, 80460); Carchi, El Pailon (1°0'7"N, 78°14'11"W), 1 ♂, 2 ♀ (MEPN 871842, 871752, 871850); El Oro, Bosque Petrificado Puyango (3°53'3"S, 80°4'41"W), 2 ♀ (TTU 102596, 103794 [TK 135290*]), El Progreso (3°19'60"S, 79°49'0"W), 2 ♂, 3 ♀ (QCAZ 2111, 2113, 2109, 2116–17), 9 mi S Zaruma (3°40'60"S, 79°37'0"W), 1 ♂ (TCWC 12283), El Faique (3°42'7"S, 79°37'18"W), 1 ♀ (TTU 102771 [TK 135391*]); Esmeraldas, Borbon comuna Corriente Grande (0°30'0"N, 79°58'0"W), 2 ♂ (QCAZ 2150, 2154), Borbon comuna Viruela (1°6'51"N, 78°59'37"W), 1 ♂, 3 ♀ (QCAZ 2168, 2173, 2178, 2181), Casa Comunal Mataje (1°12'4"N, 78°33'42"W), 1 ♀ (MEPN 882048), Chontaduro (0°55'60"N, 79°23'16"W), 1 ♂ (MEPN 851433), Comunidad Valle del Sade (0°31'0"N, 79°22'0"W), 1 ♂, 1 ♀ (MEPN 85932, 85971), E San Lorenzo, Banana Plantation (1°9'11"N, 78°27'54"W), 2 ♀ (TTU 85369–70), Esmeraldas (0°58'60"N, 79°39'20"W), 1 ♂, 2 ♀ (QCAZ 2479, 2466, 2484), Estacion Experimental La Chiquita (1°13'55"N, 78°45'57"W), 5 ♀ (TTU 85284; QCAZ 2344, 2376–77, 2380), Finca in the road from Lita to San Lorenzo (1°5'16"N, 78°41'29"W), 1 ♂ (TTU 103068), Mataje (1°21'21"N, 78°43'27"W), 2 ♂, 2 ♀ (TTU 103109–10 [TK 135905*–TK 135906*], 103107, 103196), near to Quingue (0°43'0"N, 80°4'60"W), 1 ♂, 1 ♀ (QCAZ 6070, 6072), Quininde, Rio Sade (0°19'60"N, 79°28'0"W), 1 ♀ (MEPN 85996), Rio Verde (1°4'0"N, 79°25'0"W), 1 ♂, 1 ♀ (MEPN 851431, 851436), San Francisco de Bogota (1°4'21"N, 78°42'41"W), 2 ♂ (TTU 103180–81 [TK 135701*–TK 135702*]), San Lorenzo, la Guarapera banana farm pasture (1°9'41"N, 78°28'52"W), 2 ♂, 3 ♀ (TTU 85409, 85417–19, 85370), Zapallo Grande (0°46'60"N, 78°58'60"W), 1 ♀ (QCAZ 67); Guayas, El Triunfo (2°19'0"S, 80°24'0"W), 1 ♂, 1 ♀ (QCAZ 2609, 2607), Manglares Churute (2°27'17"S, 79°37'39"W), 3 ♂, 2 ♀ (TTU 103689, 103692 [TK 134602*], 103712, 103696, 103697), Naranjal, 7 mi N of Bucay (1°30'0"S, 79°54'0"W), 1 ♂ (AMNH 62934), La Union (1°58'0"S, 80°1'0"W), 4 ♂, 2 ♀ (QCAZ 2050–51, 2055–56, 2049, 2054); Loja, 15 mi N Catacocha (4°4'0"S, 79°37'60"W), 1 ♂ (TCWC 12282); Los Rios, Buena Fe (0°54'0"S, 79°28'60"W), 1 ♂ (MEPN 81312); Manabi, Cauque River, El Destino (0°0'0"N, 80°5'60"W), 1 ♂ (AMNH 64547), Cerro Pata de Pajaro (0°1'60"N, 79°58'0"W), 1 ♂ (MEPN 913112), Parque Nacional Machalilla (1°31'0"S, 80°42'0"W), 1 ♀, 1 ♂ (MEPN 964794, 902898), Pedernales (0°4'60"N, 80°2'60"W), 1 ♀, (MEPN 913113); Pichincha, Bosque Protector La Perla (0°0'0"N, 79°22'60"W), 2 ♂, 1 ♀ (QCAZ 61, 427, 399), Nanegal (0°10'10"N, 78°40'5"W), 1 ♀ (QCAZ 1998), Santa Rosa, Rio Toachi (0°19'0"S, 78°57'0"W), 1 ♀ (QCAZ 4236), Union del Rio Toachi, Otongachi (0°25'0"S, 79°0'0"W), 1 ♂ (QCAZ 4711).

Emended diagnosis. Compared with *A. jamaicensis*, *A. aequatorialis* has a larger, broader, and more robust skull and dentition. In skull size proportion *A. j. richardsoni* is most similar to *A. aequatorialis*, while the subspecies *A. j. paulus* is the smallest form within *A. jamaicensis* followed by increased size in *A. j. parvipes*, *A. j. yucatanicus*, and *A. j. jamaicensis*. Nasals are moderately tubular in both *A. jamaicensis* and *A. aequatorialis*, with the orbitonasal shield being concave (Patten 1971). The pre- and post-orbital ridges and processes are poorly developed in *A. aequatorialis*, with a less arched and broader appearance of the rostrum with respect to *A. jamaicensis*. The zygomatic arch is more slender in *A. jamaicensis*. A higher coronoid process and longer distance from the condyle to the coronoid process is present in *A. aequatorialis* with respect with *A. jamaicensis*, and the angular process is relatively small in both taxa. Dentition is proportional to the skull size, being more robust in *A. aequatorialis*. Protocone and hypocone of the first upper molar (M1) are moderately well developed, with a wider talon in *A. aequatorialis*. In *A. aequatorialis* and *A. jamaicensis*, the second upper molar (M2) is distinctly more reduced in size and shape with paracone expanded and a developed labial cingulum (Patten 1971). Metacone and metaconule of M2 form a distinct lobe in both species. M1 and M2 are separated by a bigger gap in *A. aequatorialis*. The third lower molar (m3) is reduced in size (when present, see below) and does not show well developed cusps in either *A. aequatorialis* or *A. jamaicensis*. The dental formula in both *A. aequatorialis* and *A. jamaicensis* is I 2/2, C 1/1, P 2/2, M 2/2–3, total 30–32. Of the 134 specimens examined, *A. aequatorialis* and *A. jamaicensis* presented two upper molars and few specimens were missing the m3 in one or both sides of the mandible. Externally, *A. aequatorialis* and *A. jamaicensis* are very similar with major differences in body size proportions. For both species, the color of fur varies from pale to dark brown, with lighter color of the ventrum. Both species are characterized by a black patagium and uropatagium (Patten 1971). *Artibeus aequatorialis* has been characterized by white wing tips (Patten 1971), however, this characteristic is variable and is also present in *A. jamaicensis*. Facial stripes are not well defined in *A. aequatorialis* and are variable in *A. jamaicensis*.

Two congeneric species, *A. fraterculus* and *A. lituratus*, occur in sympatry with *A. aequatorialis*. In body and skull size, *A. aequatorialis* is intermediate between *A. lituratus* and *A. fraterculus*. *Artibeus fraterculus* is paler than *A. aequatorialis* and is known only from the Pacific slope of central-southern Ecuador and northern Peru. Nasals are not tubular, M2 is close to M1, and metacone and metaconule are not set apart from the teeth in *A. fraterculus* as in *A. aequatorialis* (Patten 1971). *Artibeus lituratus* differs mostly from *A. aequatorialis* in having a more robust, larger, and wider skull and dentition, with distinct supraorbital stripes and brownish fur (Jones 1978). The pre- and post-orbital constriction is narrower in *A. lituratus*, with the optic spicules extended.

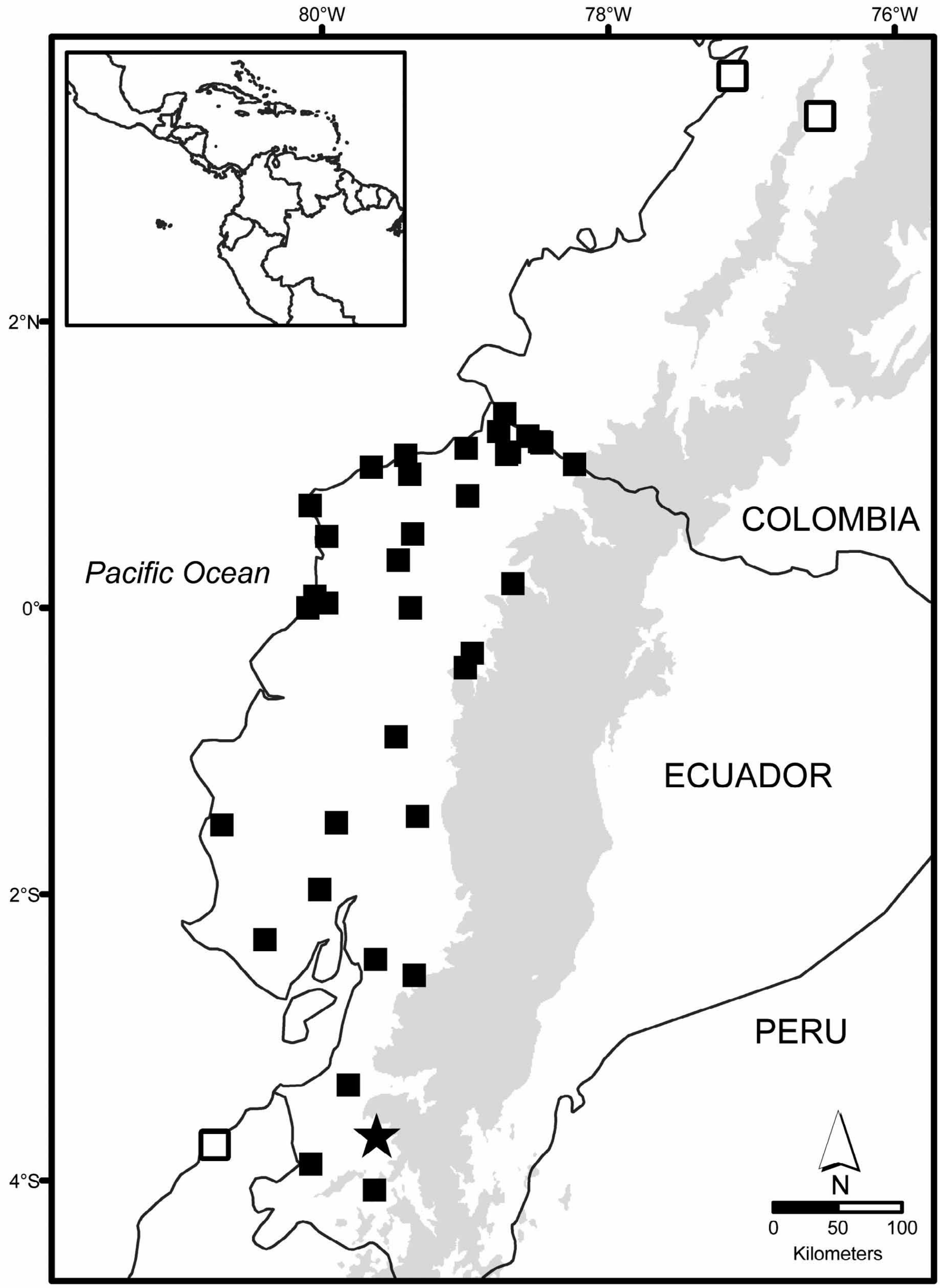

FIGURE 3. Map of the distribution of *Artibeus aequatorialis*. Star indicates the type locality of *A. aequatorialis* (Zaruma [3°40'60"S, 79°37'0"W], Ecuador). The distributional range is based on literature references (hollow squares; Andersen 1906 and Marques-Aguiar 2008) and specimens examined in the Species Account (star and solid squares). The northernmost (western Colombia; Valle del Cauca, Cali [3°26'14"N, 76°31'21"W], and Rio Raposo [3°43'0"N, 77°7'60"W]) and southernmost (western Peru; Tumbes, Faical [3°44'57"S, 80°45'2"W]) extent of *A. aequatorialis* remains to be defined. Shaded areas represent areas of the Andes Mountains higher than 1800 meters.

There has been a historical debate about the recognition of *A. planirostris* as a morphologically and genetically defined species distributed east of the Andes in South America (see Larsen *et al.* 2007). With respect to body and skull size proportion, *Artibeus aequatorialis* is smaller than *A. planirostris*, and the former differs from *A. planirostris* in skull and dentition mainly by: shape of the zygomatic arch (slender = *A. aequatorialis*; robust = *A. planirostris*); development of paracone when compared to metacone of M1 (metacone bigger than paracone = *A. aequatorialis*; metacone smaller than paracone = *A. planirostris*); location of M1 with respect to M2 (M1 and M2 separated by a large gap = *A. aequatorialis*; M1 and M2 without substantial gap = *A. planirostris*); and metacone and metaconule of the M2 (metacone and metaconule separated as a distinct lobe from rest of M2 by a fissure = *A. aequatorialis*; metacone and metaconule not separated as a distinct lobe from the rest of M2 = *A. planirostris*).

Measurements. *Artibeus aequatorialis* is larger than *A. jamaicensis* in all fourteen cranial and mandibular measurements, and is generally intermediate between *A. fraterculus* and *A. lituratus* (Appendix II).

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APPENDIX I. Additional specimens examined for morphological comparisons and genetic (AFLP) analyses (* indicates specimens used in both AFLP and morphological analyses, ** indicates specimens used only in AFLP analysis). Museum acronyms are: American Museum of Natural History, New York (AMNH), Carnegie Museum of Natural History, Pittsburgh, PA (CMNH); Museo de la Escuela Politécnica Nacional del Ecuador , Quito (MEPN); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ); Natural Science Research Laboratory of the Museum of Texas Tech University, Lubbock (NSRL; TTU = voucher number, TK = tissue number); Texas Cooperative Wildlife Collection, College Station (TCWC); and United States National Museum, Washington, D.C. (USNM).

A. fraterculus (n = 33).— Ecuador: Azuay, Challcapac, 2 ♂ (QCAZ 2246–47); El Oro, Portovelo, 1♀ (TK 135408**), Puyango, 1 ♂ (TK 135226**), Zaruma, 1 ♂ (TK 135760**); Guayas, Manglares Churute, 1 ♂ (TK 134686**), Isla Puna, 1 ♂, 1 ♀ (TK 134950**, 134947**); Manabi, Cabo Pasado, 1 ♂, 4 ♀ (QCAZ 1776, 1774–75, 1778–79); Loja, Catacocha, 1 ♂, 2 ♀ (QCAZ 1228, 1231, 1780), Mangahurquillo, 2 ♂, 4 ♀ (QCAZ 4477, 4479, 4466, 4475, 4478, 4480), San Pedro de Vilcabamba, 3 ♂, 8 ♀ (QCAZ 2255, 2266, 2268, 2251, 2254, 2256–57, 2263, 2267), Zapotillo, 2 ♂ (QCAZ 1283–84). ***A. inopinatus*** (n = 2): Honduras: Valle, 1 ♂, 1♀ (TK 101201**–02**). ***A. jamaicensis*** (n = 59).—***A. j. jamaicensis***: Dominica, Springfield State, 1 ♂, 2 ♀ (TCWC 55721, 55720, 55722); Jamaica, St. Anns Parish, 2 ♂, 1 ♀ (TK 27682*, 27686*, 27691*); Puerto Rico, Caguana, 2 ♀ (AMNH 38128, 39130), Naguabo, 1 ♀ (TTU 63276), Rio Grande, 1 ♀ (TTU 63277); St. Eustatius, 1 ♂ (TTU 102010); St. Lucia, 3 ♀ (TTU 109084–85, 109088); Union Island, 1 ♀ (TTU 105608); St. Vincent, 1 ♀ (TTU 105738). ***A. j. parvipes***: Cuba, Guantanamo, 3 ♀ (TTU 52515, 52519, 52523). ***A. j. paulus***: El Salvador, La Libertad, 1 ♂ (TCWC 21953); Guatemala, Jutiapa, 1 ♂ (AMNH 217435), Santa Rosa, 2 ♀ (AMNH 235316, 235318); Mexico, Chiapas, 3 ♀ (TCWC 8426–28). ***A. j. richardsoni***: Costa Rica, San Jose, 1 ♂, 3 ♀ (AMNH 177765, 177760, 177762, 177771); Honduras, Atlantida, 1 ♂, 1 ♀ (TK 101763**, TK 101381**), Copan, 1 ♂ (TK 101997**), Olancho, 1 ♀ (TK 102059**), Yoro, 3 ♂ (TCWC 19565–66, 19568); Nicaragua, El Castillo, 1 ♀ (TCWC 19632), La Gatiada, 1 ♂ (TCWC 8669), Madriz, 1 ♂, 1 ♀ (TCWC 8668, 21156), Matagalpa, 1 ♂, 1 ♀ (AMNH 28335, TCWC 21163), San Francisco, 1 ♂ (TCWC 8681); Panama, Canal Zone, 1 ♂, 4 ♀ (AMNH 212906, 184996, 213401–03), Chepo, 1 ♂, 1 ♀ (TCWC 12285, 12308), Chiriqui, 1 ♀ (TCWC 9632). ***A. j. yucatanicus***: Mexico, San Luis de Potosi, 2 ♂ (TCWC 28675, 30188), Yucatan, 1 ♂ (AMNH 12038); Honduras, Guanaja, 3 ♂, 1 ♀ (TCWC 14666–69). ***A. lituratus*** (n = 22).—St. Vincent and the Grenadines: Union Island, 2 ♀ (TK 128642**–43**). Honduras: Atlantida, 1 ♀ (TK 101404**). Ecuador: Esmeraldas, 1 ♂, 1♀ (USNM 113362, TK 104644**); Guayas, Balao, 3 ♂, 1 ♀ (USNM 498963–65, 498961); Los Rios, 3 ♂, 1 ♀ (USNM 498954, 522554–55, 522559, 522556); Pichincha, 2 ♂, 4 ♀ (USNM 528547, 528550, 528548–49, 528551–52); Pastaza, 1 ♀ (TK 104112**). Paraguay: Dept. Canindeyu, 1 ♂ (TK 99645**); Dept. San Pedro, 1 ♀ (TK 56994**). ***A. obscurus*** (n = 2).—Ecuador: Pastaza, 1 ♂, 1 ♀ (TK 104310**, 104001**). ***A. planirostris*** (n = 8).—Venezuela: Guarico, 1 ♂ (TK 15013**); Barinas, 1 ♀ (CMNH 78491**). Ecuador: Pastaza, 2 ♂, 4 ♀ (TK 104413**–14**, 104406**, 104410**–11**, 104419**).

APPENDIX II. Fourteen cranial and mandibular measurements (mm, acronyms defined in Materials and Methods) for females and males (sample size in parentheses) of *A. jamaicensis aequatorialis*, *A. j. jamaicensis*, *A. j. parvipes*, *A. j. paulus*, *A. j. richardsoni*, *A. j. yucatanicus*, *A. fraterculus*, and *A. lituratus* including mean, standard deviation, and range (in parentheses) where applicable.

Females

Character	*A. j. aequatorialis*	*A. j. jamaicensis*	*A. j. parvipes*	*A. j. paulus*	*A. j. richardsoni*	*A. j. yucatanicus*	*A. fraterculus*	*A. lituratus*
	n = 42	n = 12	n = 3	n = 5	n = 12	n = 1	n = 16	n = 7
GSL	29.61 ± 0.51	28.51 ± 0.57	26.61 ± 0.64	27.78 ± 0.34	29.06 ± 0.34	28.29	26.56 ± 0.32	30.66 ± 0.56
	(28.54–30.84)	(27.62–29.57)	(26.22–27.35)	(27.52–28.36)	(28.58–29.68)		(26.13–27.21)	(30.03–31.52)
CIL	26.54 ± 0.57	25.52 ± 0.72	23.75 ± 0.48	24.52 ± 0.12	25.89 ± 0.28	25.14	23.45 ± 0.39	27.40 ± 0.55
	(25.51–27.75)	(24.46–26.53)	(23.44–24.31)	(24.40–24.71)	(25.43–26.36)		(22.65–24.17)	(26.87–28.42)
SH	13.00 ± 0.36	12.65 ± 0.45	12.01 ± 0.39	12.49 ± 0.32	12.91 ± 0.29	12.16	11.82 ± 0.34	13.67 ± 0.50
	(12.29–13.96)	(12.02–13.34)	(11.70–12.45)	(12.04–12.83)	(12.41–13.38)		(11.29–12.45)	(13.21–14.43)
MB	15.50 ± 0.44	14.93 ± 0.49	14.47 ± 0.29	14.88 ± 0.18	15.50 ± 0.47	14.59	14.33 ± 0.38	16.95 ± 0.63
	(14.35–16.25)	(14.10–15.60)	(14.17–14.74)	(14.65–15.06)	(14.77–16.32)		(13.44–14.88)	(15.58–17.51)
BRW	13.93 ± 0.32	13.40 ± 0.60	12.99 ± 0.41	13.36 ± 0.19	13.97 ± 0.40	13.45	13.06 ± 0.19	14.89 ± 0.44
	(13.28–14.61)	(12.28–14.09)	(12.69–13.46)	(13.11–13.62)	(13.43–14.76)		(12.79–13.39)	(14.23–15.71)
ZB	17.97 ± 0.52	17.28 ± 0.70	16.16 ± 0.15	16.77 ± 0.47	17.92 ± 0.52	16.59	16.09 ± 0.26	19.02 ± 0.74
	(16.63–18.99)	(16.35–18.31)	(15.99–16.28)	(16.10–17.31)	(17.14–18.98)		(15.54–16.46)	(18.13–20.51)
POW	7.40 ± 0.31	7.58 ± 0.19	7.18 ± 0.37	7.49 ± 0.27	7.48 ± 0.31	7.27	6.58 ± 0.17	6.67 ± 0.33
	(6.85–8.01)	(7.33–7.98)	(6.92–7.60)	(7.07–7.71)	(6.99–8.05)		(6.21–6.81)	(6.24–7.12)
C1C1	8.52 ± 0.26	7.83 ± 0.24	7.45 ± 0.07	7.65 ± 0.14	8.27 ± 0.25	7.96	7.37 ± 0.16	8.76 ± 0.24
	(7.92–9.05)	(7.41–8.22)	(7.39–7.52)	(7.41–7.76)	(7.89–8.67)		(7.09–7.71)	(8.34–9.14)
M2M2	13.35 ± 0.36	12.58 ± 0.45	11.81 ± 0.08	11.97 ± 0.46	12.96 ± 0.26	11.78	11.81 ± 0.28	13.56 ± 0.57
	(12.83–14.22)	(12.01–13.27)	(11.72–11.88)	(11.25–12.46)	(12.57–13.46)		(11.35–12.34)	(12.81–14.58)
PL	14.35 ± 0.37	13.57 ± 0.45	11.64 ± 0.75	13.04 ± 0.29	13.79 ± 0.43	12.98	12.27 ± 0.30	14.56 ± 0.53
	(13.65–15.19)	(12.83–14.14)	(11.18–12.50)	(12.72–13.39)	(13.00–14.55)		(11.60–12.86)	(14.09–15.39)
MXTR	10.48 ± 0.31	10.09 ± 0.27	9.32 ± 0.24	9.64 ± 0.14	10.36 ± 0.20	9.76	9.26 ± 0.22	10.93 ± 0.30
	(9.77–11.08)	(9.66–10.48)	(9.10–9.57)	(9.46–9.85)	(10.04–10.71)		(8.80–9.66)	(10.45–11.36)
MIL	19.45 ± 0.46	18.52 ± 0.52	17.29 ± 0.66	17.66 ± 0.41	18.85 ± 0.33	17.66	16.87 ± 0.25	20.45 ± 0.47
	(18.54–20.36)	(17.58–19.19)	(16.77–18.03)	(17.13–18.12)	(18.50–19.78)		(16.42–17.42)	(19.79–21.04)
MLT	11.62 ± 0.36	10.89 ± 0.43	10.10 ± 0.18	10.60 ± 0.28	11.36 ± 0.30	9.87	10.25 ± 0.22	12.19 ± 0.26
	(10.47–12.36)	(10.33–11.56)	(9.92–10.27)	(10.12–10.84)	(11.05–12.00)		(9.95–10.65)	(11.80–12.53)
c1c1	4.73 ± 0.21	4.45 ± 0.23	4.18 ± 0.18	4.17 ± 0.22	4.68 ± 0.20	4.29	4.30 ± 0.16	4.98 ± 0.19
	(4.39–5.30)	(4.12–4.82)	(4.00–4.35)	(3.87–4.39)	(4.36–5.15)		(4.07–4.71)	(4.67–5.22)

Males

Character	*A. j. aequatorialis*	*A. j. jamaicensis*	*A. j. paulus*	*A. j. richardsoni*	*A. j. yucatanicus*	*A. fraterculus*	*A. lituratus*
	n = 37	n = 4	n = 2	n = 10	n = 6	n = 11	n = 9
GSL	29.43 ± 0.53	27.95 ± 0.35	28.02 ± 0.52	28.87 ± 0.39	27.41 ± 0.52	26.78 ± 0.50	30.91 ± 0.97
	(27.88–30.63)	(27.60–28.42)	(27.65–28.39)	(28.20–29.44)	(26.84–28.13)	(25.80–27.65)	(29.10–32.41)
CIL	26.37 ± 0.51	24.98 ± 0.40	25.04 ± 0.79	25.80 ± 0.50	24.33 ± 0.44	23.59 ± 0.65	27.15 ± 0.75
	(24.82–27.50)	(24.45–25.32)	(24.48–25.60)	(24.76–26.63)	(23.68–24.75)	(22.16–24.71)	(26.06–28.08)
SH	13.12 ± 0.40	12.68 ± 0.35	12.16 ± 0.22	12.94 ± 0.37	12.28 ± 0.41	11.92 ± 0.40	13.90 ± 0.49
	(12.27–13.91)	(12.25–13.10)	(12.00–12.31)	(12.21–13.39)	(11.47–12.56)	(11.40–12.57)	(13.05–14.45)
MB	15.55 ± 0.38	14.74 ± 0.42	14.72 ± 0.28	15.36 ± 0.31	14.54 ± 0.25	14.50 ± 0.30	16.81 ± 0.37
	(14.32–16.60)	(14.23–15.26)	(14.52–14.92)	(14.79–15.75)	(14.12–14.78)	(13.95–14.84)	(16.26–17.31)
BRW	13.96 ± 0.33	13.28 ± 0.24	13.45 ± 0.05	13.79 ± 0.26	13.35 ± 0.10	13.15 ± 0.27	14.84 ± 0.33
	(12.78–14.60)	(13.02–13.53)	(13.41–13.48)	(13.27–14.08)	(13.23–13.46)	(12.67–13.48)	(14.19–15.25)
ZB	17.87 ± 0.52	16.79 ± 0.42	17.19 ± 0.45	17.62 ± 0.48	16.75 ± 0.36	16.27 ± 0.35	18.86 ± 0.54
	(16.66–18.93)	(16.20–17.11)	(16.87–17.51)	(16.83–18.16)	(16.20–17.24)	(15.55–16.88)	(18.12–19.60)
POW	7.35 ± 0.21	7.44 ± 0.36	7.14 ± 0.47	7.51 ± 0.28	7.35 ± 0.18	6.61 ± 0.23	6.56 ± 0.31
	(6.94–7.77)	(7.12–7.94)	(6.80–7.47)	(6.94–7.87)	(7.13–7.66)	(6.27–6.96)	(6.06–6.91)
C1C1	8.64 ± 0.31	7.89 ± 0.29	7.91 ± 0.02	8.32 ± 0.22	8.01 ± 0.34	7.48 ± 0.21	8.72 ± 0.27
	(7.85–9.20)	(7.48–8.10)	(7.89–7.92)	(7.90–8.58)	(7.69–8.60)	(7.06–7.73)	(8.46–9.30)
M2M2	13.40 ± 0.36	12.43 ± 0.14	12.14 ± 0.21	12.87 ± 0.29	12.33 ± 0.51	11.88 ± 0.33	13.64 ± 0.41
	(12.62–14.16)	(12.25–12.60)	(11.99–12.29)	(12.34–13.23)	(11.58–13.06)	(11.30–12.26)	(13.06–14.53)
PL	14.24 ± 0.38	13.28 ± 0.52	13.07 ± 0.70	13.73 ± 0.45	12.66 ± 0.43	12.43 ± 0.52	14.48 ± 0.41
	(13.15–14.89)	(12.76–13.97)	(12.57–13.56)	(12.76–14.36)	(12.12–13.07)	(11.50–13.21)	(14.01–15.00)
MXTR	10.64 ± 0.33	10.01 ± 0.18	9.88 ± 0.22	10.42 ± 0.19	9.63 ± 0.22	9.30 ± 0.32	11.02 ± 0.26
	(9.88–11.39)	(9.87–10.28)	(9.72–10.03)	(10.10–10.71)	(9.29–9.90)	(8.61–9.59)	(10.65–11.47)
MIL	19.38 ± 0.42	18.11 ± 0.17	18.00 ± 0.88	18.82 ± 0.31	17.54 ± 0.30	16.88 ± 0.53	20.23 ± 0.50
	(18.31–20.55)	(17.98–18.36)	(17.37–18.62)	(18.39–19.41)	(17.09–17.95)	(15.67–17.57)	(19.57–20.90)
MLT	11.74 ± 0.33	10.83 ± 0.08	11.08 ± 0.25	11.49 ± 0.25	10.71 ± 0.21	10.39 ± 0.32	12.13 ± 0.32
	(10.86–12.56)	(10.76–10.90)	(10.90–11.26)	(11.10–11.94)	(10.51–11.10)	(9.75–10.91)	(11.59–12.71)
c1c1	4.79 ± 0.21	4.49 ± 0.11	4.52 ± 0.01	4.64 ± 0.19	4.42 ± 0.25	4.32 ± 0.21	4.94 ± 0.14
	(4.37–5.14)	(4.39–4.60)	(4.51–4.53)	(4.33–4.92)	(4.12–4.75)	(4.07–4.63)	(4.74–5.16)