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A taxonomic revision of the Yasuni Round-eared bat, *Lophostoma yasuni* (Chiroptera: Phyllostomidae)

M. ALEJANDRA CAMACHO[1,*], DANIEL CHÁVEZ[2] & SANTIAGO F. BURNEO[1]

[1]*Sección Mastozoología, Museo de Zoología, Pontificia Universidad Católica del Ecuador, Av. 12 de Octubre 1076, Quito, Ecuador. E-mails: mailto:macamachom@puce.edu.ec (MAC), sburneo@puce.edu.ec (SFB)*

[2]*Department of Ecology and Evolutionary Biology, University of California at Los Angeles, 610 Charles E. Young Drive South, Los Angeles, California 90095-1601, U.S.A. E-mail: dechavezv@g.ucla.edu (DC)*

[3]*Corresponding author*

Abstract

The Yasuni Round-eared bat, *Lophostoma yasuni*, was described in 2004 by morphological analysis of the holotype, the only specimen attributed to this taxon to date. A molecular analysis using cytochrome-*b* sequences and a new morphological analysis that includes the holotype of *L. yasuni* and two specimens of *L. carrikeri* from near the type locality of *L. yasuni* were carried out. The new molecular and morphological evidence places *L. yasuni* within the clade of *L. carrikeri*. We propose that *L. yasuni* should therefore be considered as a synonym of *L. carrikeri.* An emended diagnosis for *L. carrikeri* extending ranges of craniodental measurements for this species is presented.

Key words: Ecuador, synonymy, systematics, taxonomy, Yasuni National Park

Resumen

El Murciélago de orejas redondas de Yasuní, *Lophostoma yasuni*, fue descrito en 2004 a partir del análisis morfológico del holotipo, el único espécimen colectado de ese taxón hasta la fecha. Se realizó un análisis molecular basado en citocromo-*b* y una nueva revisión morfológica que incluyó el holotipo de *L. yasuni* y dos especímenes de *L. carrikeri* recientemente colectados en las cercanías a la localidad tipo de *L. yasuni.* La nueva evidencia sitúa a *L. yasuni* dentro del clado de *L. carrikeri.* Proponemos que *L. yasuni* sea considerado un sinónimo de *L. carrikeri*. Se presenta una diagnosis corregida para *L. carrikeri* que amplía los rangos de las medidas cráneo-dentales reportadas para esta especie.

Palabras clave: Ecuador, Parque Nacional Yasuní, sinonimia, sistemática, taxonomía

Introduction

The Round-eared bats (genus *Lophostoma* d'Orbigny, 1836) have a wide distribution in Middle and South America, ranging from southern Mexico to southwestern Paraguay (Simmons 2005; Williams & Genoways *et al.* 2008). This genus was considered a synonym of *Tonatia* Gray, 1827 until Lee *et al.* (2002) showed that the group was paraphyletic and recommended to restrict the species *bidens* and *saurophila* to *Tonatia* and the remaining taxa to *Lophostoma.*

Currently, eight species are recognized within *Lophostoma* d'Orbigny, 1836: *L. brasiliense* Peters, 1867; *L. carrikeri* (Allen 1910); *L. evotis* (Davis & Carter 1978); *L. kalkoae* Velazco & Gardner 2012; *L. occidentalis* (Davis & Carter 1978); *L. schulzi* (Genoways & Williams 1980); *L. silvicolum* d'Orbigny, 1836; and *L. yasuni* Fonseca & Pinto, 2004.

Three of these species, *L. carrikeri, L. kalkoae,* and *L. yasuni* are characterized by the presence of white ventral fur across the chest and abdomen, bordered laterally by pale brown fur on the sides of the body (McCarthy *et al.* 1992; Fonseca & Pinto 2004; Velazco & Cadenillas 2011; Velazco & Gardner 2012). Two of the white-chested

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species, *L. yasuni* and *L. carrikeri*, have been reported from the Yasuni National Park, Eastern Ecuador (Fonseca & Pinto 2014; Camacho *et al.* 2014).

Lophostoma yasuni was described by Fonseca & Pinto (2004) from a single individual, an adult male (QCAZ 4935 [holotype]), collected near the Estación Científica Yasuní, in Orellana Province, Ecuador. The holotype includes the skin and an incomplete skull lacking lower incisors, lower canines, second and third lower premolars, and the auditory bullae. No further individuals of this species have been recorded since March, 2001.

Based on its description, *L. yasuni* exhibits the following diagnostic characters: wings, ears, and interfemoral membrane are darker than in the other *Lophostoma*; lack of white margins in the ears, which are conspicuous in most *L. carrikeri*; a shorter forearm (43.9 mm) and a larger skull (25.9 mm) than in *L. carrikeri*; ears without post-auricular patches and a hairy base of the thumb; rostrum robust and depressed posteriorly, with the paraoccipital processes well-developed; sagittal crest moderately developed; robust upper toothrows bowed outward; and a slender mandible in comparison to *L. carrikeri*.

The original description compared *L. yasuni* with other species of the genus, especially *L. carrikeri*, of which 21 specimens were examined; however, no molecular analysis was available. Similarly, other studies aiming to identify phylogenetic relationships within *Lophostoma* have not included molecular data of the *L. yasuni* holotype (Velazco & Cadenillas 2011).

Herein, new evidence is presented on the status of *L. yasuni* including molecular and morphological data from additional specimens of *L. carrikeri* representing new locality records in order to test the status of *L. yasuni*.

Materials and methods

This study aims to evaluate the taxonomic status of *Lophostoma yasuni*, by complementing the analysis previously carried out by Velazco & Cadenillas (2011), on the evolutionary relationships of the Round-eared bats. This will be achieved by adding new Ecuadorian material to the specimens and tissues analyzed in 2011.

Molecular analysis. A total of 33 cytochrome-*b* sequences were analyzed in this study. Twenty-six sequences of *Lophostoma* and outgroups (*Phyllostomus hastatus*, *Tonatia bidens*, *Tonatia saurophila*, and *Vampyrum spectrum*) that were used by Velazco & Cadenillas (2011) were retrieved from GenBank, and joined with cytochrome-*b* sequences of three Ecuadorian specimens, including the holotype of *L. yasuni* and two *L. carrikeri.* GenBank accession numbers for the three new sequences generated by this study are provided in Table 1.

DNA was extracted from dried skin snippets of a 13-year old museum specimen, the *Lophostoma yasuni* holotype (QCAZ4935). Samples were obtained from the forearm and lower lip. The extraction protocol was modified from de Moraes-Barros & Morante (2007). We performed a Guanidine Thiocyanate procedure (Bilton & Jaarola 1996) instead of the Phenol protocol. Furthermore, all DNA extraction procedures included one duplicate set of negative control tube (blank extract) containing only digestion reagents. DNA from the Ecuadorian *Lophostoma carrikeri* specimens was extracted following the salt-precipitation method (Bilton & Jaarola 1996) from liver samples initially preserved in 95% ethanol and later frozen and stored at –80°C.

Purified *Lophostoma* DNA from Ecuadorian specimens was used to amplify 1,147 bp fragments of the mitochondrial cytochrome-*b* gene. The following primer pairs were used: forward primer glo7L (5'-CAYCGTTGTATTTCAACTRTAAGAAC-3') and reverse primer glo6H (5'-CGGTGTAATGRATATACTACAT RG-3') (Hoffmann & Baker 2001). Thermal profile for the cytochrome-*b* gene PCR followed Hoffmann & Baker (2001). In order to determine the quality of the amplicons, PCR products were electrophoresed on 1% agarose gels stained with SYBR® Safe. Any unconsumed dNTPs and primers remaining in the PCR product mixture were removed with the ExoSAP-IT method. Negative control was amplified and sequenced to detect any trace of foreign DNA. The Sanger sequencing was carried out through Macrogen Inc.

Edition and assembly of sequences were performed with Geneious 5.4.7 (Biomatters Ltd, Auckland, New Zealand, www.geneious.com) and aligned using the ClustalW tool. All alignments were inspected visually to correct any errors and to ensure that they were not "pseudogenes" (Rouchka & Cha 2009). The best partition strategies along with the corresponding models of evolution were obtained in PartitionFinder 1.1.1 (Lanfear *et al.* 2012) under the Bayesian information criterion. In order to estimate the evolutionary rate of base substitutions, a Kimura 2-parameter model (Kimura 1980) was employed. The analyses involved 33 nucleotide sequences (29 *Lophostoma*, including the new ones, and four outgroups). All positions containing gaps or missing data were eliminated. There were a total of 1,065 positions in the final dataset.

TABLE 1. Species, tissues collection numbers, and GenBank accession numbers for the analyzed *Lophostoma* and outgroup species. Ecuadorian *Lophostoma carrikeri* and *L. yasuni* were added to the samples used by Velazco & Cadenillas (2011).

Taxon	Museum/Tissue numbers	Country	Genbank accession number
L. brasiliense	F38605	Guyana	FJ1554486
L. brasiliense	F38112	Panama	JF923842
L. carrikeri	QCAZ13578	Ecuador	KU886210
L. carrikeri	QCAZ13994	Ecuador	KU886211
L. carrikeri	F39143	Guyana	JF923843
L. carrikeri	F39537	Guyana	JF923844
L. evotis	TK101727/TTU84384	Honduras	JF923846
L. evotis	FN29417	Mexico	JF923845
L. evotis	FN29496	Mexico	FJ155491
L. occidentalis	TK104505/TTU85277/QCAZ9103	Ecuador	JF923848
L. occidentalis	TK104520/TTU85292/QCAZ6500	Ecuador	JF923849
L. occidentalis	MUSM19334	Peru	JF923847
L. schulzi	F35126	Guyana	JF923850
L. schulzi	F38318	Guyana	FJ155485
L. silvicolum	NK25209	Bolivia	JF923851
L. silvicolum	TK104132/TTU84904/QCAZ6602	Ecuador	JF923855
L. silvicolum	TK104158/TTU84930	Ecuador	JF923856
L. silvicolum	F34947	Guyana	FJ155492
L. silvicolum	F38068	Panama	JF923858
L. silvicolum	F38067	Panama	JF923857
L. silvicolum	TK56635	Paraguay	JF923852
L. silvicolum	TK56716	Paraguay	FJ155493
L. silvicolum	TK22709	Peru	JF923860
L. silvicolum	FMNH203542	Peru	JF923859
L. silvicolum	TK10279	Suriname	JF923853
L. silvicolum	TK10403	Suriname	JF923854
L. silvicolum	TK19191	Venezuela	JF923861
L. silvicolum	TK19233	Venezuela	JF923862
L. yasuni [a]	QCAZ4935	Ecuador	KU886212
Tonatia bidens	MVZ185959	Brazil	JF923863
Tonatia saurophila	F36877	Guyana	JF923864
Phyllostomus hastatus	CMNH78333	Venezuela	FJ155479
Vampyrum spectrum	TTU61071/TK40370	Honduras	FJ155482

[a] Holotype of *Lophostoma yasuni*

To infer the phylogenetic relationships of *Lophostoma* species from South America and the position of *Lophostoma yasuni* within the gene tree, maximum-likelihood (ML) and Bayesian Inference (BI) approaches were used. ML analysis was conducted using GARLI v.2.0 (Zwickl 2006). Nodal support was determined by 1000 bootstrap replicates. Bootstrap values above 70% were considered well supported (Hillis & Bull 1993). The BI analysis was performed using Markov Chains Monte Carlo (MCMC) through MrBayes 3.2.2 (Ronquist *et al.* 2012). Four Markov chains were run twice for 10,000,000 generations. Trees were sampled every 1,000 generations resulting in 20,000 saved trees per analysis. Adequacy of chain mixing was assessed by examining the effective sample sizes (ESS) in Tracer, with ESS > 200 considered as satisfactory and plotting the –ln L per

generation. After analyzing convergence, chain mixing, and sampling, the first 1,000 trees in the sample were discarded as "burn-in". The remaining trees were used to obtain a consensus tree by the 50% majority rule in Mesquite 3.0. Posterior probabilities above 0.95 were considered strongly supported.

Morphological analysis. The present analysis focuses on species of white-bellied *Lophostoma*. Craniodental measurements taken from Ecuadorian specimens of *L. carrikeri* and the holotype of *L. yasuni* were united with the original measurements used in Velazco & Cadenillas (2011). These include: FA—forearm length; MET-III—metacarpal III length; GLS—greatest length of skull; CIL—condyloincisive length; CCL—condylocanine length; BB—braincase breadth; ZB—zygomatic breadth; PB—postorbital breadth; C–C—palatal width at canines; MSTW—mastoid width; MPW—mastoid process width; PL—palatal length; MTRL—maxillary toothrow length; MLTRL—molariform toothrow length; M2–M2—width at M2; DENL—dentary length, MANDL—mandibular toothrow length; COH—coronoid height. The description of each measurement is provided by Velazco & Cadenillas (2011).

A total of 18 white-bellied *Lophostoma* were analyzed (Table 2): 15 *L. carrikeri* (11 females, 4 males); 2 *L. kalkoae* (1 female, 1 male), and the holotype of *L. yasuni* (male).

TABLE 2. Measurements (mm) and sample statistics[a] of white-bellied Round-eared bats. Measurements descriptions are provided in the materials and methods section (Morphological analysis).

Character	*L. carrikeri* (n=15)	*L. kalkoae*[b] (n=2)	*L. yasuni* (n=1)
FA	45.7±1.5 (42.2–47.7)	44.6, 45.8	43.9
GLS	24.2±0.9 (23.0–25.3)	23.2, 23.8	26.6
MET III	37.7±1.4 (34.1–40.0)	35.7, 36.1	37.3
CIL	20.9±0.6 (19.8–21.9)	19.8, 20.4	23.0
CCL	20.2±0.6 (19.0–21.3)	19.2, 19.6	21.0
BB	9.6±0.3 (9.0–10.3)	9.5, 9.5	10.0
ZB	11.1±0.4 (10.3–12.1)	11.4, 11.2	12.7
PB	3.7±0.2 (3.3–4.1)	3.6, 3.9	4.0
C–C	4.4±0.2 (4.1–4.8.)	4.3, 4.7	5.5
MSTW	9.6±0.3 (9.0–10.2)	9.5, 9.4	10.0
MPW	11.5±0.5 (10.8–12.8)	11.3, 11.3	12.0
PL	10.5±0.5 (9.2–11.1)	9.9, 10.1	10.0
MTRL	8.2±0.2 (7.7–8.6)	7.9, 8.0	9.4
MLTRL	6.9±0.3 (6.5–7.3)	6.4, 6.7	6.0
M2–M2	7.5±0.3 (7.1–7.9)	7.5, 7.5	8.80
DENL	14.9±0.6 (13.8–15.9)	14.3, 14.7	16.90
MANDL	9.2±0.3 (8.6–9.7)	9.0, 9.1	11.0
COH	5.5±0.3 (5.0–6.0)	5.1, 5.5	7.0

[a] Summary statistics [mean and standard deviation (first line), observed range (second line)] of measurements for *L. carrikeri* and *L. kalkoae* (see Appendix for a list of specimens measured); only one measurement is reported for *L. yasuni* since only the holotype specimen is available for this species.
[b] First measurement corresponds to *Lophostoma kalkoae* Paratype (EKV 119); second measurement corresponds to *L. kalkoae* Holotype (USNM 582249)

It is noteworthy that the measurement of greatest length of skull reported by Fonseca & Pinto (2004) followed Simmons & Voss (1998) limits, from the posteriormost point on the occiput to the anteriormost point on the premaxillae, excluding the incisors. In order to obtain comparable data, here we used the criterion of Velazco & Cadenillas (2011), which does include incisors.

A correlation matrix was built to perform a Principal Component Analysis (PCA) in order to assess sexual dimorphism, reported for *L. carrikeri* by McCarthy *et al.* (1983), comparing males and females within *L. carrikeri*, including *L. yasuni* to test if it falls within *L. carrikeri* range of measurements. A similar PCA was performed to

evaluate phenetic variation within white-bellied *Lophostoma* independently of gender. Analyses were carried out in R-Wizard (Guisande 2012).

Results

Molecular analysis. The Bayesian inference and Maximum-Likelihood analyses produced similar, well supported topologies (Figure 1). The holotype of *L. yasuni* (QCAZ 4935) appears nested within the clade of *L. carrikeri*.

The genetic distance among specimens of *L. carrikeri* averages 1.46%, while the mean pairwise distance between the holotype of *L. yasuni* and the *L. carrikeri* clade is 1.38% (Table 3).

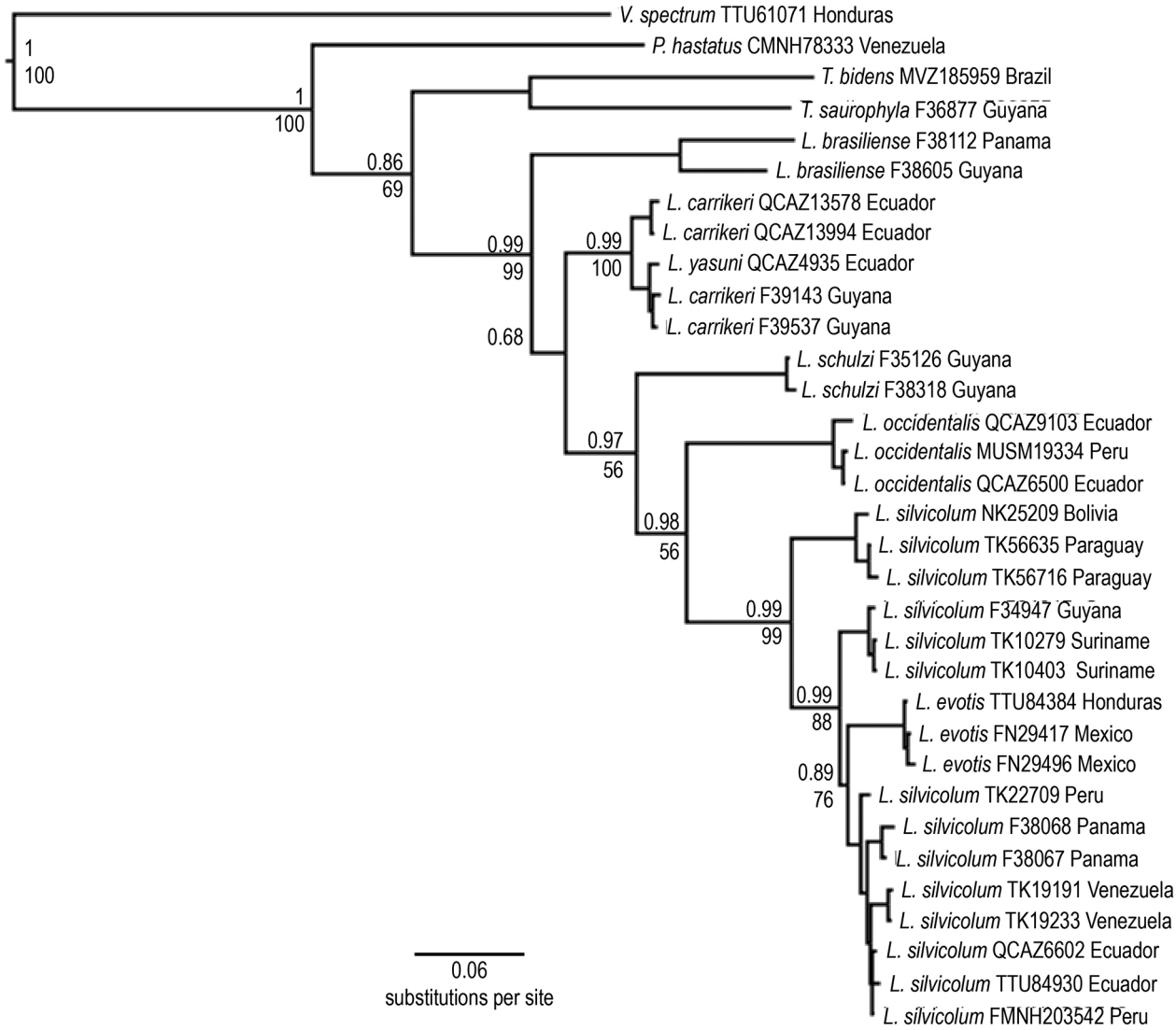

FIGURE 1. Phylogenetic relationships within *Lophostoma* based on Maximum-likelihood and Bayesian inference derived from the mitochondrial gene cytochrome-*b*. Nodal support is represented by posterior probabilities (above nodes), and bootstrap values (below nodes).

Morphological analysis. The PCA analysis performed to display sexual dimorphism in *L. carrikeri* showed a biplot with an unclear tendency (Figure 2). The first principal component represents overall size, in which females have generally higher scores, and males show lower ones, but not forming definitive groups. The *L. yasuni* holotype (a male) has the lower value recorded on PC1. The second principal component has most of the females grouping towards the lower scores, along with *L. yasuni,* and most of the males fell towards the higher end, where most of the shape measurements, such as forearm length, lie. PC1 and PC2 show a cumulative proportion of variance of 76.2%.

TABLE 3. Corrected pairwise cytochrome-*b* sequence divergence (%) among *Lophostoma* clades. Values along the diagonal represent intraspecific divergence. Standard error estimates are shown in parenthesis.

	1	2	3	4	5	6	7
1 – *L. carrikeri*	1.46 (±0.25)						
2 – *L. yasuni*	1.38 (± 0.25)	-					
3 – *L. brasiliense*	12.78 (± 0.97)	12.95 (± 1.01)	8.98 (±1.01)				
4 – *L. evotis*	13.31 (± 1.29)	13.57 (± 1.33)	15.19 (± 1.08)	0.38 (±0.15)			
5 – *L. occidentalis*	15.51 (± 1.28)	15.23 (± 1.33)	15.40 (± 1.14)	13.93 (± 1.32)	1.02 (±0.21)		
6 – *L. schulzi*	12.75 (± 1.21)	12.34 (± 1.19)	14.20 (± 1.05)	13.79 (± 1.35)	12.61 (± 1.21)	0.47 (±0.23)	
7 – *L. silvicolum*	14.05 (± 1.24)	13.86 (± 1.29)	15.57 (± 1.07)	5.02 (± 0.49)	14.22 (± 1.26)	14.22 (± 1.32)	4.02 (±0.41)

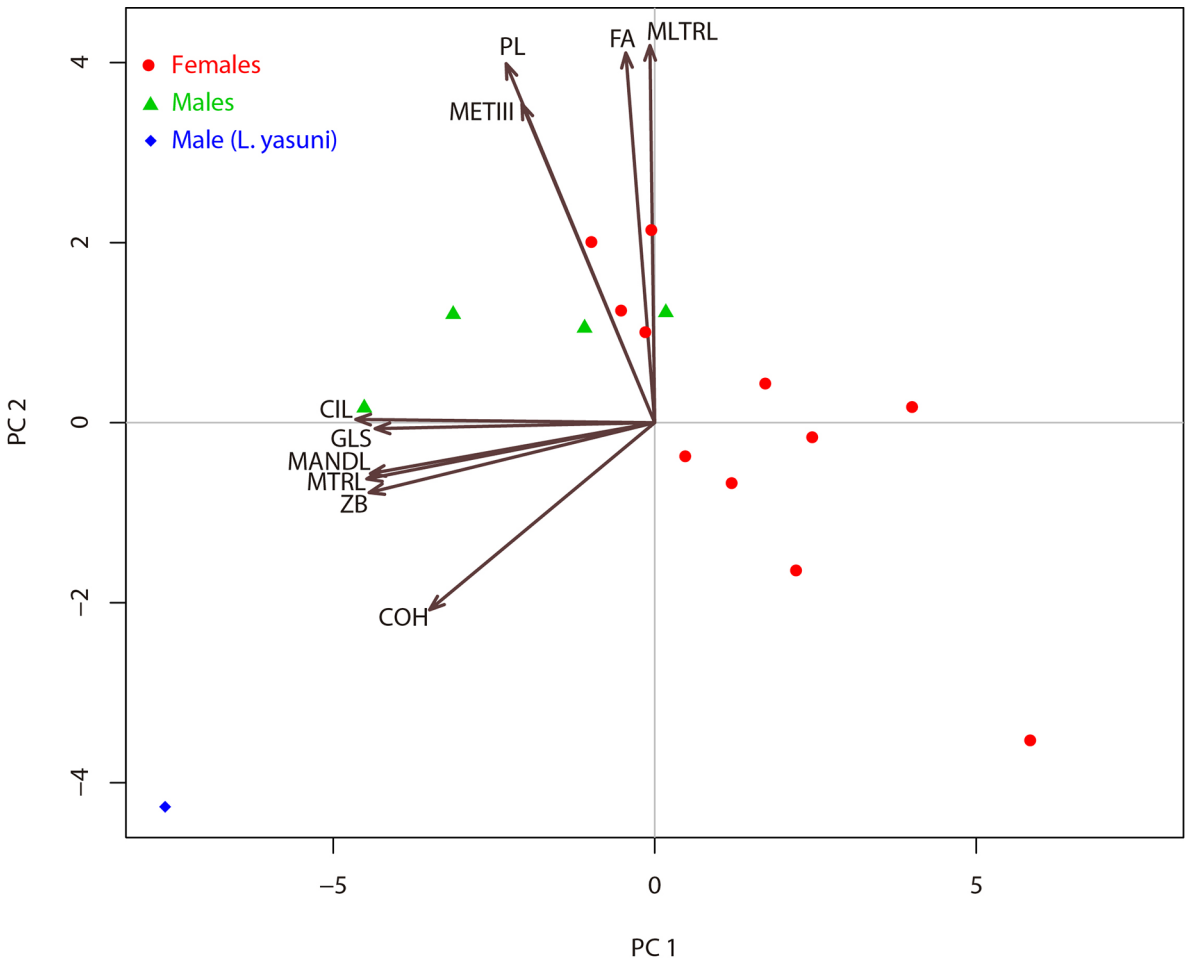

FIGURE 2. Principal component analysis for sex differences in *Lophostoma carrikeri* and *L. yasuni* based in 18 external and craniodental measurements. PCA results presented are a combined representation of measurements and variables.

The PCA of craniodental variation among the species of white-bellied *Lophostoma* shows a pattern where *L. kalkoae* fell within *L. carrikeri* along both PC1 (regarded as size) and PC2 (regarded as shape). *L. yasuni* is separated from the other species with a higher score on PC1, associated with measurements such as GLS, CIL,

MTRL, MANDL, and COH. On PC2, *L. yasuni* has lower scores, not associated with size measurements such as FA, METIII, PL, and MTRL (Figure 3). Together, the first two principal components represent 75.7% of total variance (Table 4).

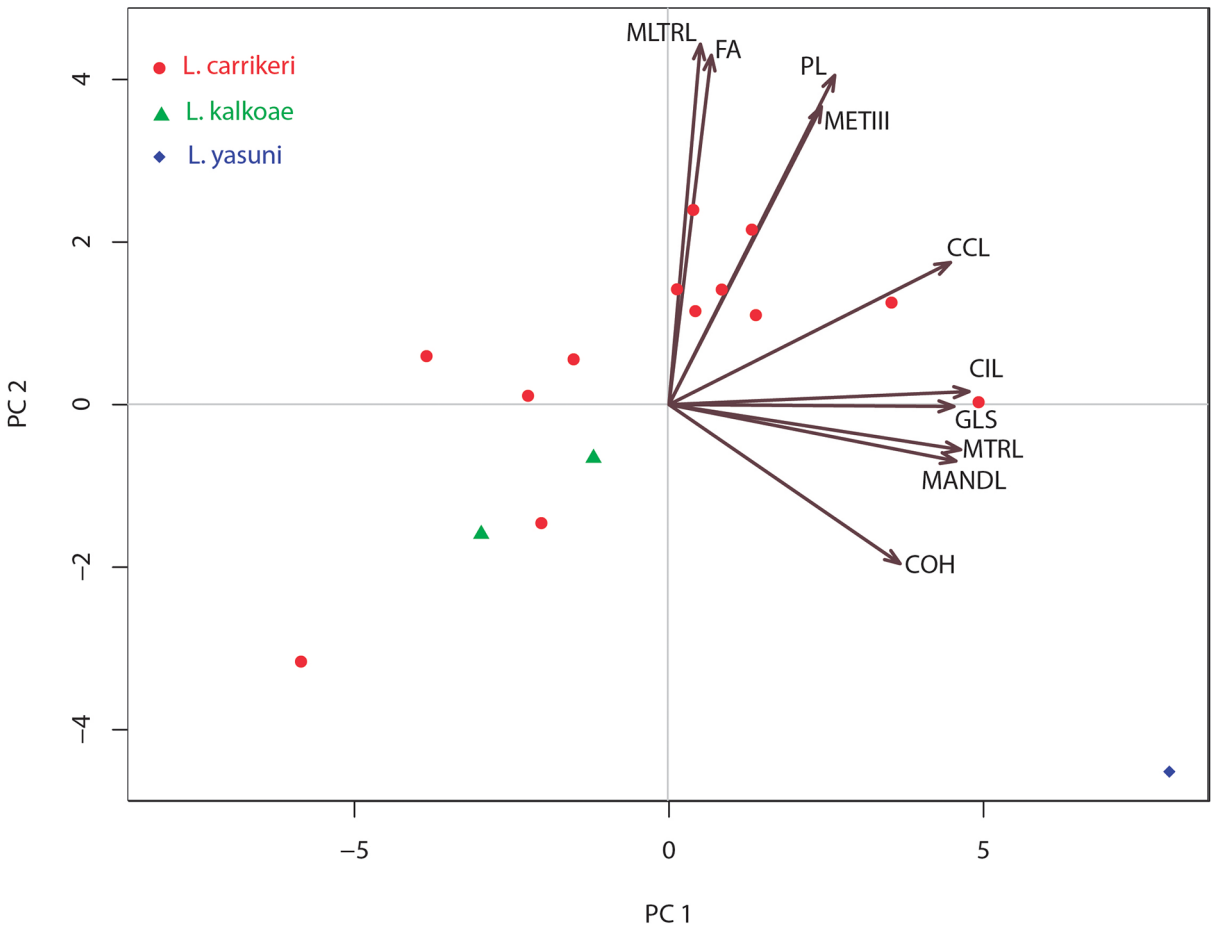

FIGURE 3. Principal component analysis to test phenetic variation within *Lophostoma carrikeri, L. kalkoae*, and *L. yasuni* based in 18 external and craniodental measurements. PCA results presented are a combined representation of measurements and variables.

Discussion

Arguments against species delimitation based on one or a few specimens is not recent (see Winston 1999; Dayrat 2005; Valdecasas *et al.* 2008; Lim *et al.* 2012). One of the arguments opposing it is that a species should not be described until intra- and inter-specific character variation has been comprehensively addressed. We agree with Valdecasas *et al.* (2008) in thinking that this task is virtually impossible, even where thousands of individuals of a given taxon are available in natural history collections.

A recent survey of taxonomic literature from 2000 to 2010 showed that rare species are not an uncommon phenomenon in systematics, where 17.7% of described invertebrates in that period of time and 19% of vertebrates are known only from a single specimen (Lim *et al*. 2012).

Taxonomists continually find themselves in the position of deciding if the target taxon (even in the case of singletons) is an undescribed species. No matter which species concept is used and which operational criteria is chosen for delimitation, the final result of any species definition is a hypothesis that can be dismissed if newly available data refutes it (Valdecasas *et al.* 2008).

Certainly, authors and reviewers of the Yasuni Round-eared bat agreed that this unique specimen had a particular set of morphological characters that made it an unlikely member of an already described species. As is common practice (see Lim *et al.* 2012), the delimitation of this species based only on its morphology involved an

implicit probability argument. The validity of that argument is evident in the morphological results that we obtained, where the holotype is clearly different from other white-bellied round-eared bats.

Here, molecular evidence obtained a decade after the description of *Lophostoma yasuni* and new morphological analyses that include newly collected specimens of white-bellied *Lophostoma* from the same locality in Ecuador have allowed us to refute the hypothesis that *L. yasuni* represents an independent evolutionary lineage. We suggest that it should be consider a synonym of *L. carrikeri* based on our analyses of molecular and morphological evidence.

TABLE 4. Factor loadings for the first three principal components of the PCA analysis from 18 external and craniodental measurements (variables) of *L. carrikeri* and *L. yasuni.* Description of each measurement is provided by Velazco & Cadenillas (2011).

	Factor loadings		
Variable	PC1	PC2	PC3
FA	0.042	0.473	0.257
METIII	0.152	0.404	0.269
GLS	0.283	-0.002	0.060
CIL	0.298	0.018	0.104
CCL	0.280	0.193	-0.030
BB	0.254	-0.027	-0.389
ZB	0.272	-0.139	-0.121
PB	0.193	0.006	-0.174
CC	0.254	-0.142	0.228
MSTW	0.249	0.039	-0.431
MPW	0.206	-0.023	-0.441
PL	0.165	0.446	-0.018
MTRL	0.290	-0.061	0.170
MLTRL	0.031	0.489	-0.241
M2M2	0.251	-0.186	0.203
DENL	0.271	-0.066	0.162
MANDL	0.285	-0.076	0.245
COH	0.230	-0.216	0.046
Proportion of variance (%)	57.68%	17.99%	7.80%
Cumulative proportion	57.68%	75.67%	83.47%

Molecular evidence. A rare species could, in principle, be recognized from similar ones if its DNA sequence is so distinct that it would not cluster together with sequences of other species (Lim *et al.* 2012). In the present work, evidence of clustering is clearly visible and would have been evident in 2004, when the species was described, if a similar analysis had been carried out.

The nucleotide sequences in the cyt-*b* gene of *L. carrikeri* and *L. yasuni* differ by 1.38% (Table 3), indistinguishable from the 1.46% shown between individuals of *L. carrikeri*. Other currently recognized *Lophostoma* species (exception for the pair *L. silvicolum* and *L. evotis*) differ in this sequence by 12.61–15.51% (Table 3). The low genetic distance data and short phylogenetic branch length observed between the holotype of *L. yasuni* and *L. carrikeri* is further evidence of them belonging to the same taxon. According to Bradley & Baker (2001), a genetic distance lower than 2% is typical of interspecific variation.

We did not include nuclear genes, not only because sequences to compare are scarce, but because unless the chosen nuclear markers are of neutral evolution, the retrieved information would be less informative if a recent speciation event is to be proven (Puorto *et al*, 2001). However, there is no doubt that the now proposed taxonomic hypothesis can be corroborated, or not, with additional molecular information.

Morphological evidence. The only evidence that *Lophostoma yasuni* constitutes a distinct species comes from

the morphological analysis in its description. Fonseca & Pinto (2004) found that some craniodental and external measurements of the holotype were distinct from *L. carrikeri*. In fact, both the principal component analysis performed by Velazco & Cadenillas (2011) and in the present study, involving additional specimens, consistently showed the separation of the *L. yasuni* specimen from other groups. However, descriptive statistics allowed us to confirm that many of the variables of *L. yasuni* do not fall entirely outside the known ranges of *L. carrikeri* analyzed measurements.

Sample size could explain the resulting patterns and it is worth mentioning that this group of bats is very rare and difficult to capture by standard or widely used collecting methods, so further collecting efforts will shed light on pattern definition. We strongly support the idea that this single specimen of *L. yasuni* is an anomalous individual with unusual craniodental dimensions. Clearly, there is a risk of naming a new species on the base of a single individual. Although there is no rule on how many specimens should be analyzed before naming a new species, there is a probability that a single specimen might be a form that would only extend a known range of measurements.

McCarthy *et al.* (1983) showed that males are significantly larger than females in nine of twelve cranial measurements. PC scores in this study tend to support a difference for sexual dimorphism (Figure 2); nevertheless, the sample size of males and females might skew the results.

According to the *L. yasuni* description, one expects that *L. carrikeri* skulls will be smaller than in the holotype specimen, but larger specimens of *L. carrikeri* have been reported in literature (Goodwin 1942; Genoways & Williams 1980), including individuals even larger than *L. yasuni* (McCarthy *et al.* 1992; Lim *et al*. 1999). Therefore, one of the most important diagnostic characters of *L. yasuni* such as larger skull dimension proves to be unreliable when more data are analyzed.

Fonseca & Pinto (2004) also considered the smaller size of the forearm as a diagnostic character. An evaluation of the measurements reported for *L. carrikeri* showed that the forearm of *L. yasuni* is only 0.2 mm shorter than the smallest measurement reported for *L. carrikeri* in countries other than Ecuador (Velazco & Gardner 2012), but fall within measurements recently reported for *L. carrikeri* in Ecuador (Camacho *et al.* 2014). This character is also unreliable, supporting the hypothesis that variation within *L. carrikeri* is larger than previously known.

The color of wings, ears and interfemoral membrane of *L. yasuni,* diagnosed as dark brown or blackish, may be part of the color range variation, without diagnostic value. The same coloration is mentioned for *L. carrikeri* in its description and subsequent revisions (Allen 1910; McCarthy *et al.* 1992).

These considerations lead us to ponder the other cranial measurements and shapes of basisphenoid pits, upper toothrows, and mandibles reported by Fonseca & Pinto (2004) as nothing but variations of *L. carrikeri.* Velazco & Gardner (2012) did not use the basisphenoid pits as diagnostic characters for *L. carrikeri*, a comparative feature to *L. kalkoae* since this character is variable in *L. carrikeri* and, although stable in *L. kalkoae*, that species is currently known from only two specimens.

Based on the presented evidence we propose an emended description of *Lophostoma carrikeri*. This diagnosis is based on the data retrieved from morphological specimens analyzed.

Systematics

Family Phyllostomidae Gray, 1825

Subfamily Phyllostominae Gray, 1825

Genus *Lophostoma* d'Orbigny, 1836

Lophostoma carrikeri (Allen, 1910)

Carriker's Round-eared Bat
Figure 4

Chrotopterus carrikeri Allen, 1910:147; type locality "Rio Mocho" Bolívar, Venezuela.
Tonatia carrikeri Goodwin, 1942:207; name combination.
Lophostoma carrikeri: Lee, Hoofer, and Van Den Bussche, 2002:55; first use of current name combination.

Lophostoma yasuni Fonseca and Pinto, 2004:1; type locality "vicinity of the Yasuní Research Station (00°30'S, 75°55'W, 220 m), Yasuní National Park and Biosphere Reserve, Province of Orellana, Ecuador."
L[*ophostoma*]. *yasuni*: Tirira, 2007: 278 name combination.

Distribution. *Lophostoma carrikeri* is restricted to South America, known from Brazil, French Guiana, Suriname, Guyana, Venezuela, Colombia, Ecuador, Peru, and Bolivia (Figure 5).

Emended diagnosis. *Lophostoma carrikeri* is a medium size round-eared bat (FA 42.2–47.7 mm, GLS 23.0–26.6 mm; CCL 19.0–21.3 mm). *L. carrikeri* is larger than *L. brasiliense* and *L. schulzi*, but smaller than *L. evotis*, *L. occidentalis*, and *L. silvicolum*. All measurements overlap with those of *L. kalkoae* and *L. schulzi* (Table 2). Craniodental measurements including variation from recently recorded specimens are presented in Table 5.

TABLE 5. Mean, standard deviation, and range of external and craniodental measurements for *Lophostoma carrikeri*, including *L. yasuni* as a junior synonym of *L. carrikeri*.

Character	Measurement (in mm) (n=16)
FA	45.6 ± 1.5 (42.2–47.7)
GLS	24.3 ± 0.9 (23.0–26.6)
MET III	37.7 ± 1.4 (34.1–40.0)
CIL	21.0 ± 0.8 (19.8–23.0)
CCL	20.3 ± 0.7 (19.0–21.3)
BB	9.6 ± 0.3 (9.0–10.3)
ZB	11.2 ± 0.6 (10.3–12.7)
PB	3.8 ± 0.2 (3.3–4.1)
C–C	4.5 ± 0.3 (4.1–5.5)
MSTW	9.6 ± 0.3 (9.0–10.2)
MPW	11.6 ± 0.5 (10.8–12.8)
PL	10.5 ± 0.5 (9.2–11.1)
MTRL	8.3 ± 0.4 (7.7–9.4)
MLTRL	6.8 ± 0.3 (6.0–7.3)
M2–M2	7.6 ± 0.4 (7.1–8.8)
DENL	15.0 ± 0.7 (13.8–16.9)
MANDL	9.3 ± 0.6 (8.6–11.0)
COH	5.6 ± 0.5 (5.0–7.0)

L. carrikeri is easily identified by its plain white ventral fur from the throat through the abdomen, bordered along the flanks by the gray-brown dorsal fur (Figure 4). Dorsal pelage is long and tricolored, with pale to whitish tips. Nose-leaf, chin, and base of the ears are blackish brown. These characters are shared with *L. kalkoae* although the latter has dark brown gular fur, whereas in *L. carrikeri* this region is pale to whitish. *L. carrikeri* lacks the white to pale post-auricular patches connected to the chest by a band of pale hairs present in *L. kalkoae*, *L. occidentalis*, and *L. evotis*. Ears are light brown to blackish with or without a whitish narrow margin. Proximal third of the dorsal surface of the forearm is sparsely haired; ventrally, forearm and adjacent membrane covered with short grayish hairs.

Skull length ranges from 23.0 to 26.6 mm (Table 5). The skull is constricted postorbitally and is slightly concave in the orbital region; sagittal crests may vary, from well-developed in adult males to moderately developed or absent in females and young males (Allen 1910; Goodwin 1942; McCarthy *et al.* 1992). Lateral development of the mastoid region is moderate. Short palatal length with posterior margin aligned with second molars. Upper medial incisors well developed and convergent. Shallow indentation on the lingual cingulum of the upper canine. P3 well developed. Posterior lingual cusp on P4 cingulum is weakly developed. M1 and M2 parastyles are absent. Lingual cingulum on both M1 and M2 is also absent. p3 well developed and in line with toothrow.

FIGURE 4. *Lophostoma carrikeri*, adult female. QCAZ 13578. Location: Boanamo, Waorani Ethnic Reserve, Yasuni National Park. Photo courtesy of Diego Tirira.

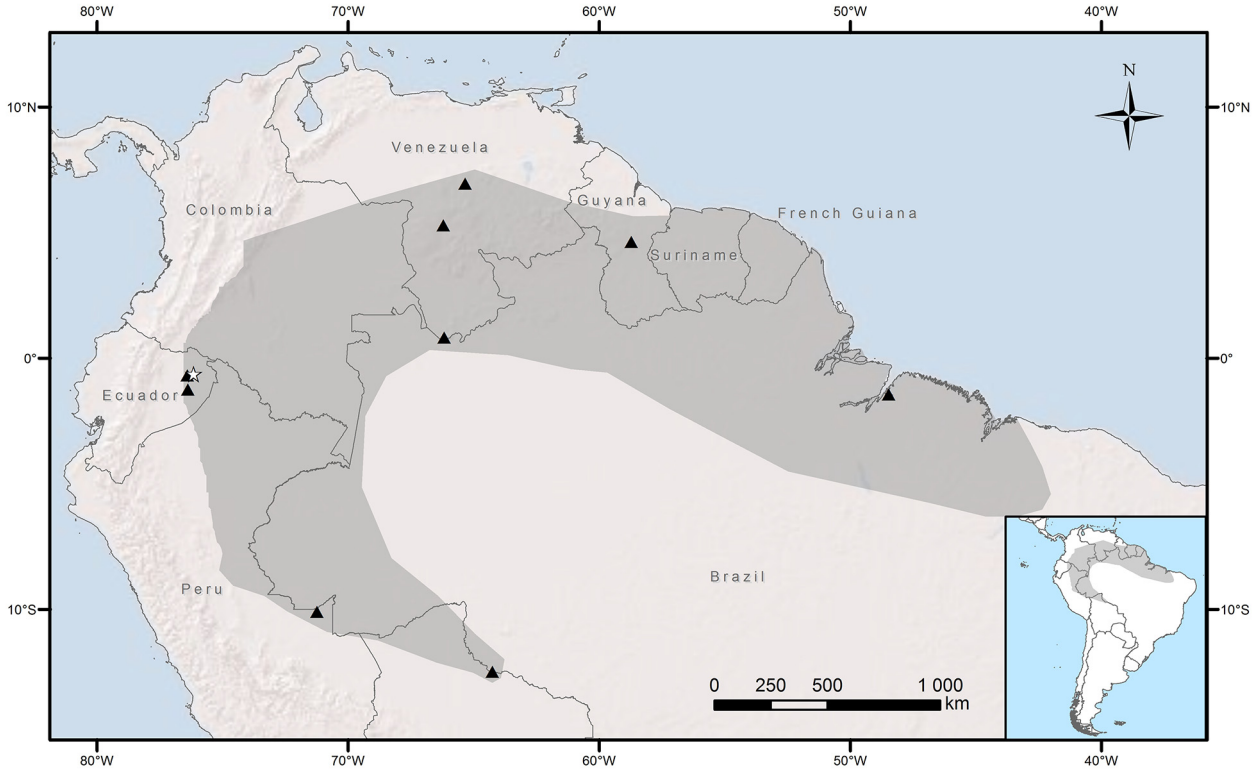

FIGURE 5. Distribution of *L. carrikeri,* modified from Camacho *et al*. (2014). The star marks the type locality of *L. yasuni*. Triangles mark the locations of samples used in the genetic and morphological analyses.

Comparisons. Relative to other *Lophostoma* species, *L. carrikeri* and *L. kalkoae* can be easily distinguished by the presence of pure white fur from the throat to the lower abdomen, bordered on the sides of the body by brown hair. These species are not known to occur in sympatry, but comparisons are made in case white-bellied *Lophostoma* are discovered on the western versant of the Andes in South America.Molecular evidence shows that many Neotropical bats from Central America appear more closely related to samples from the western versant of the Andes than to those from the eastern versant (Patterson *et al.* 1992; Hoffmann & Baker 2001, 2003; Hoffmann *et al.* 2003; Fonseca *et al.* 2007; Larsen *et al.* 2007).

Despite the fact that all linear measurements of *L. kalkoae* overlap with those of *L. carrikeri*, some features differentiate these species. Gular fur is dark brown in *L. kalkoae* but pale to whitish in *L. carrikeri*. *L. kalkoae* has pale gray post-auricular patches, absent in *L. carrikeri.* Dorsal surface of the proximal third of the forearm in *L. carrikeri* is sparsely covered with hair, and rather naked in *L. kalkoae*.

In most features, the skull of *L. carrikeri* resembles that of *L. kalkoae.* Both species show slender rostra with a postorbital constriction. Lateral mastoid process is moderately developed in *L. carrikeri*, but less developed in *L. kalkoae*. Being larger, *L. carrikeri* may show more robust rostra and well developed lateral mastoid processes than *L. kalkoae*. *L. carrikeri* presents smaller incisors than *L. kalkoae*, resembling them in shape and direction. *L. carrikeri* shows a weak indentation on the lingual cingulum of the upper canine, deeply marked in *L. kalkoae*. P3 is short and less developed in *L. carrikeri*, whereas tall and well developed in *L. kalkoae*. Posterior lingual cusp on the cingulum of P4 less developed in *L. carrikeri*. *L. carrikeri* lacks a lingual cingulum in M1, unlike *L. kalkoae*. Other dental characters are equivalent in size and shape with those of *L. kalkoae*.

Natural history. No amendments are needed regarding the natural history of *L. carrikeri*. This species has been associated with mesic and riparian forests in lowlands (McCarthy & Handley Jr 1988) and has been captured in Igapó, Varzea, semideciduous savanna, and dry forest in the Amazon Basin (McCarthy & Handley Jr 1988; Gribel & Taddei 1989; Bernard & Fenton 2002; Sampaio *et al.* 2003; Castro-Arellano *et al.* 2007; Gregorin *et al.* 2008). Also, Zortéa *et al.* (2009) reported *L. carrikeri* in a transitional locality between a semideciduous forest and a riparian forest in the Cerrado Brazil. Apparently, the species prefers undisturbed forests. In Ecuador, *L. carrikeri*

has been captured in primary terra firme forests with an understory of mature woody and herbaceous vegetation (Camacho *et al.* 2014) in the Yasuni National Park, as well as in primary and secondary tropical rainforest with an understory mainly of immature woody and herbaceous vegetation (Fonseca & Pinto 2004).

L. carrikeri may prefer hollowed termite nests as reported by Allen (1911) and McCarthy *et al.* (1983). Specimens from Ecuador were captured in ground level mist nets. Neither new behavioral traits nor diet information is available. Three records of ectoparasitic arthropods were collected from a specimen of *Lophostoma carrikeri* in Yasuni National Park, Ecuador, the first report of this species from Ecuador (Camacho *et al.* 2014): *Stizostrebla longirostris* Jobling, 1939; *Pseudostrebla sparsisetis* Wenzel, 1976; and *Mastoptera* sp. Two of these, *Stizostrebla longirostris* and *Pseudostrebla sparsisetis*, are exclusively known to parasitize *Lophostoma carrikeri.*

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APPENDIX. List of specimens examined in this study with their respective localities.

Lophostoma carrikeri (16)

BOLIVIA: Beni: Mamore, opposite Costa Marques, Brazil, Río Itenez (AMNH 209322). **BRAZIL:** Para: Belem, Mocambo, Igapo (USNM 393005); Belem, Varzea (USNM 460095). **ECUADOR**: Orellana: vicinity of the Yasuní Research Station, Yasuní National Park (QCAZ 4935, *L. yasuni* [holotype]); Boanamo, Waorani Ethnic Reserve, near the Yasuni National Park (QCAZ 13578); Ceiba trail at the Yasuni Research Station, Yasuni National Park (QCAZ 13994). **PERU:** Ucayali: Balta, Río Curanja (LSUMZ 14076–14077). **VENEZUELA:** Amazonas: San Juan, 163 Km ESE Pto. Ayacucho, Río Manapiare (USNM 407274); Cerro Neblina Base Camp, Río Mawarinuma (USNM 560556); Bolivar: Cedeno. Río Mocho (AMNH 30177–30180, 30182–30183).

Lophostoma kalkoae (2)

PANAMA: Colón: Soberania National Park, Pipeline Road near the former Limbo Hunt Club (EKVK 119; USNM 582249 [holotype]).