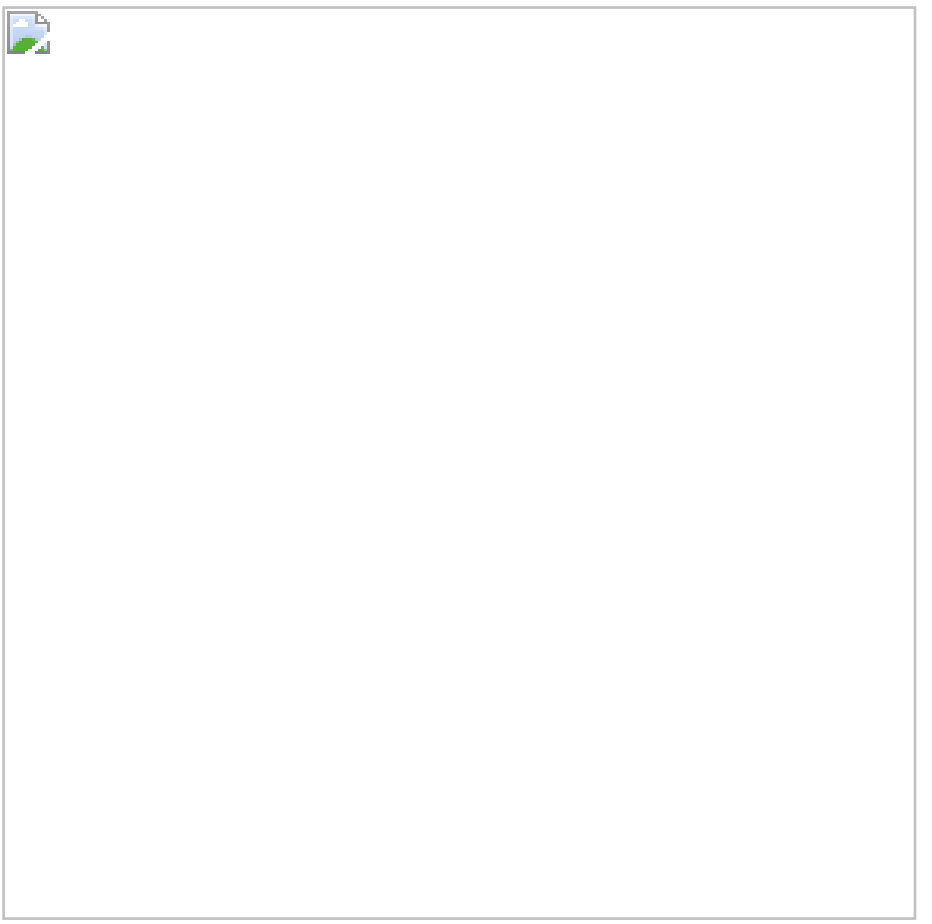

Systematics and Taxonomy of Great Striped-Faced Bats of the Genus Vampyrodes Thomas, 1900 (Chiroptera: Phyllostomidae)

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Systematics and Taxonomy of Great Striped-Faced Bats of the Genus *Vampyrodes* Thomas, 1900 (Chiroptera: Phyllostomidae)

PAÚL M. VELAZCO[1] AND NANCY B. SIMMONS[1]

ABSTRACT

The Neotropical bat genus *Vampyrodes* (Chiroptera: Phyllostomidae: Stenodermatinae) is widely distributed from southern Mexico to southeastern Brazil. Long thought to be monotypic, *V. caraccioli* Thomas, 1889, was recognized by previous authors as including two subspecies with the nominate form inhabiting South America south and east of the Andes, and another subspecies, *V. c. major* Allen, 1908, occurring west and north of the Andes. Reexamination of these forms using molecular and morphological methods supports recognition of these lineages as distinct at the species level. We here provide amended descriptions and diagnoses for these taxa. We also report for the first time an example of *perikymata* (incremental growth lines that appear on the surface of dental enamel as a series of grooves) in Chiroptera. Presence of distinct perikymata is a synapomorphy of the genus *Vampyrodes*.

INTRODUCTION

The Neotropical bat genus *Vampyrodes* (figs. 1–2) is a monotypic taxon of frugivorous bats distributed from southern Mexico to southeastern Brazil. Although it has an extensive distribution, members of this genus seem to be rare in lower latitudes (Velazco et al., 2010a). *Vampyrodes* is distinguished from related taxa in the subfamily Stenodermatinae by the combination

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of six characteristics: relatively large body size (>25 g; FA = 47–59 mm); presence of bright white facial stripes and a white mid-dorsal stripe extending from the crown of the head to the rump; presence of a fringe of hair on the trailing edge of the uropatagium; presence of three lower molars and two upper molars; and presence of two accessory cusps on the posterior edge of the second upper premolar.

The species presently known as *Vampyrodes caraccioli* was originally described as a member of the genus *Vampyrops*. Thomas (1889) described *Vampyrops Caracciolæ* based on a speci-

FIGURE 1. Photograph of an adult male *Vampyrodes caraccioli* (showing facial and dorsal stripes) captured at a clay lick along the Rio Tiputini, Yasuni National Park, Ecuador, in November 2008. Photograph by Bejat McCracken.

FIGURE 2. Photograph of an adult male *Vampyrodes caraccioli* (showing the two genal vibrissae) captured at a clay lick along the Rio Tiputini, Yasuni National Park, Ecuador, in November 2008. Photograph by Bejat McCracken.

men from Trinidad in which he noted two sets of diagnostic characteristics that distinguished it from other species of *Vampyrops*: unusually conspicuous facial and dorsal stripes that are brighter and more prominent than those in other species of that genus, and the presence of two upper and lower incisors and two upper and three lower molars. Thomas named this species after Henry Caracciola, who had collected the holotype. Soon after the description of *Vampyrops Caracciolæ*, Thomas realized that the correct name of the collector was H. Caracciolo, not Caracciola, and because of this error Thomas (1893a) changed the name to *Vampyrops Caraccioli*. Husson (1954), however, argued that *caracciolae* was the correct original spelling and that Thomas's (1893a) emendation to *caraccioli* was unjustified. Goodwin and Greenhall (1961) emended *caraccioli* to *caraccioloi* based upon Pittier and Tate's (1932) and Cabrera's (1958) use of that same spelling. However, according to Carter and Dolan (1978) the correct Latin genitive singular case for the name Caracciolo, derived from the Latin nominative *Caracciolus*, should be *Caraccioli*. All studies published after Carter and Dolan's (1978) interpretation of the nomenclature have followed those authors in using *V. caraccioli* for this taxon.

Eleven years after describing *V. caraccioli*, Thomas (1900) named *Vampyrodes* as a subgenus of *Vampyrops* Thomas, 1889 (= *Platyrrhinus* Saussure, 1860). As conceived by Thomas (1900), *Vampyrops* included four subgenera differentiated by the number of incisors and molars: *Vampyrops* (including *dorsalis* Thomas, 1900; *infuscus* Peters, 1880; *lineatus* Geoffroy St.-Hilaire, 1810; *vittatus* Peters, 1859; and *zarhinus* Allen, 1891), *Vampyriscus* (for *bidens* Dobson, 1878), *Vampyressa* (for *pusillus* Wagner, 1843), and *Vampyrodes* (for *Caraccioli* Thomas, 1889). Miller (1907) later elevated *Vampyodes* to the genus level, justifying this decision on the absence of M3 and the considerable reduction of the metacone in M2.

One year later, Allen (1908) described *Vampyrodes major* from a specimen from Panama, highlighting the larger size of *V. major* with respect to *V. caraccioli*. Subsequently, Thomas (1924) described *Vampyrodes ornatus* from five specimens collected in Peru by Latham Rutter, but he did not acknowledge the existence of any other species or specimens of *Vampyrodes* other than *V. caraccioli* from Trinidad (Thomas, 1889, 1893b), restricting the description of *V. ornatus* to a comparison only with *V. caraccioli*.

After the description of the three nominal taxa of *Vampyrodes*, several classification arrangements have been proposed. Cabrera (1958) recognized two species—*V. caraccioli* and *V. major*—with *V. caraccioli* including two subspecies, *V. c. caraccioli* and *V. c. ornatus*. Starrett and Casebeer (1968) recognized two species—*V. caraccioli* and *V. major*—with *ornatus* regarded as a junior synonym of *major*. In the most recent classification, authors have recognized *Vampyrodes* as a monotypic genus with two subspecies (*V. c. caraccioli* and *V. c. major*), with *ornatus* regarded as a junior synonym of *major* (Handley, 1966; Jones and Carter, 1976; Koopman, 1993, 1994; Simmons, 2005; Gardner, 2008).

In this paper, we explore the systematics of the genus *Vampyrodes* across its entire geographic range. We analyze molecular, morphometric, and morphological data to clarify the evolutionary history, species limits, and taxonomy of *Vampyrodes*.

MATERIAL AND METHODS

Our approach in this study was first to identify different lineages based on gene sequences, and subsequently to examine voucher specimens to investigate patterns of morphological congruence with the molecular patterns previously detected. The specimens examined and tissues used for this study belong to the following collections:

AMNH	American Museum of Natural History, New York
BMNH	British Museum (Natural History), London, UK
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
FMNH	Field Museum of Natural History, Chicago, Illinois
ALP	Field numbers of Adriano Lúcio Peracchi, Instituto de Biologia, Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil
IavH-M	Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Boyacá, Colombia
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MUSM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, California
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
TTU (TK)	Museum of Texas Tech University, Lubbock, Texas
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UV	Sección de Zoología, Departamento de Biología, Universidad del Valle, Cali, Colombia

Molecular Analyses

To evaluate the relationships among taxa of the genus *Vampyrodes*, we sequenced the complete cytochrome-*b* gene (1140 base pairs; eight specimens) and D-loop (412 base pairs; nine individuals) from different localities in Central and South America. We also sequenced one specimen of *Platyrrhinus recifinus* for both markers to serve as an outgroup. In addition, five sequences of cyt-*b* and three of D-loop of *Vampyrodes,* and one sequence each for *Chiroderma villosum* and *Vampyressa melissa,* were retrieved from GenBank. The sequences of *Chiroderma*, *Platyrrhinus*, and *Vampyressa* were used as outgroup taxa to root trees (table 1).

DNA isolation and sequencing were performed either in the Pritzker Laboratory for Molecular Systematic and Evolution of the Field Museum of Natural History (USA) or in the Laboratório de Biodiversidade e Evolução Molecular of the Universidade Federal de Minas Gerais (Brazil), depending on the sample. We used different protocols in each lab as described below.

Pritzker Laboratory for Molecular Systematic and Evolution: Total genomic DNA from tissue samples was isolated from a small (~0.05 g, wet weight) portion of liver or muscle samples that had been frozen or preserved in lysis buffer or ethanol. DNA was extracted

TABLE 1. Species, tissue collection number, and GenBank Accession Numbers for the *Vampyrodes* and outgroup samples used in this study.

Taxon	Tissue/Collection Numbers[a]	Locality[b]	GenBank Accession Numbers	
			Cyt-*b*	D-loop
Chiroderma villosum	FMNH 174652	Peru: Madre de Dios (107)	FJ154121	FJ154253
Platyrrhinus recifinus	MVZ 185607	Brazil: São Paulo (109)	HQ637415	HQ637424
Vampyressa melissa	FMNH 174910	Peru: Cuzco (110)	FJ154185	FJ154317
Vampyrodes caraccioli	MZUSP 34655	Brazil: São Paulo (8)	HQ637416	HQ637425
Vampyrodes caraccioli	TK 25083 / CM 94707	Trinidad and Tobago: Trinidad (58)	AY157034	HQ637426
Vampyrodes caraccioli	TK 25024 / TTU 44102	Trinidad and Tobago: Trinidad (58)	HQ637417	HQ637427
Vampyrodes caraccioli	MVZ 166596	Peru: Madre de Dios (40)	HQ637418	HQ637428
Vampyrodes caraccioli	MVZ 192683	Peru: Madre de Dios (40)	HQ637419	HQ637429
Vampyrodes caraccioli	FMNH 174912	Peru: Madre de Dios (40)	FJ154182	FJ154314
Vampyrodes caraccioli	FMNH 174913	Peru: Madre de Dios (40)	HQ637420	HQ637430
Vampyrodes caraccioli	FMNH 174914	Peru: Cuzco (20)	FJ154183	FJ154315
Vampyrodes caraccioli	FMNH 174915	Peru: Madre de Dios (40)	FJ154184	FJ154316
Vampyrodes caraccioli	TK 22860 / TTU 46306	Peru: Cuzco (20)	HQ637421	HQ637431
Vampyrodes caraccioli	TK 70540 / USNM 582872	Peru: Cuzco (20)	DQ312407	N/A
Vampyrodes major	TK 7849 / TTU 30642	Nicaragua: Zelaya (89)	HQ637422	HQ637432
Vampyrodes major	TK 7851 / TTU 30643	Nicaragua: Zelaya (89)	HQ637423	HQ637433

[a] Alphanumeric identifiers used by institutional tissue collections (and to label terminal in accompanying tree; fig. 4). See Material and Methods for names of museums collections identified by abbreviations in this table.
[b] Country and next-largest administrative unit (stated, department, province, etc). Numbers in parentheses refer to gazetteer entries (appendix), which provide additional geographic information.

using a Puregene DNA isolation kit (Gentra System, Minneapolis, Minnesota). Polymerase chain reaction (PCR) and sequencing reactions were carried out with primers L14724 and H15915 from Irwin et al. (1991) and L0 and E3 from Douzery and Randy (1997) and Huchon et al. (1999). PCR conditions include an initial denaturation step at 95°–94° C for 3–5 min, followed by 35 cycles of PCR. The cycles involved denaturation at 95° C for 30 s, annealing at 50°–52° C for 30–90 s, polymerization at 68°–72° C for 1–2 min, and a final extension at 72° C at 5–8 min. The PCR reagents in a 25 µl sample were 2 µl of FMNH Taq, 2.5 µl 10× reaction buffer, 2.5 µl of 8 mM premixed deoxynucleotide triphosphates, 15 µl of ddH_2O, 1 µl per primer (10 µM), and 1 µl genomic DNA. The PCR products were cycle-sequenced using ABI PRISM Big Dye v. 3.1 (Applied Biosystems, Foster City, CA). The cycling protocol used involved an initial denaturation step at 96° C for 60 s, followed by 25 cycles of denaturation at 96° C for 10 s, annealing at 50° C for 5 min, and extension at 60° C for 4 min. Cycle-sequencing products were purified through an EtOH–EDTA precipitation protocol and run on an ABI PRISM 3730 Genetic Analyzer (Applied Biosystems, Foster City, CA) using the amplification primers. Sequences were edited and compiled using Sequencher™ 4.1.2 software (Gene Codes). Base-calling ambiguities between strands were resolved by choosing the call on the cleanest strand.

Laboratório de Biodiversidade e Evolução Molecular: DNA extractions were performed using the QIAGEN DNeasy kit (QIAGEN, Valencia, CA, USA). PCR amplifications were carried out in 15 µl reactions containing 40–80 ng of DNA, buffer 1B (Phoneutria: 1.5 mM $MgCl_2$, 10 mM Tris–HCl [pH 8.4], 50 mM KCl, 0.1% Triton X–100), 200 µM dNTPs set (Amersham–Biosciences), 0.5 µM of primers and 1.25 U of Taq DNA polymerase (Phoneutria). The primers were the same used in the Pritzker Laboratory.

PCR conditions included an initial denaturation step at 95°–94° C for 3–5 min, followed by 35 cycles of PCR. The cycles involved denaturation at 95° C for 30 s, annealing at 50°–52° C for 30–90 s, polymerization at 68°–72° C for 1–2 min, and a final extension at 72° C at 5–9 min. PCR products were purified using a solution of 20% polyethylene glycol 8000 in 2.5 M of NaCl using a protocol described by Sambrook et al. (2001).

Sequencing of both strands was carried out in a MegaBACE 1000 (GE Healthcare) automated sequencer using DYEnamic ET Terminator kits (GE Healthcare) and the same primers used in PCR amplifications. Sequences were assembled and checked for quality using a combination of the programs Phred v.0.20425 (Ewing et al., 1998; Ewing and Green, 1998) and Phrap v.0.990319 (Green, 1994), and the assembled chromatograms were verified and edited using Consed 12.0 (Gordon et al., 1998).

All sequences generated in this study have been deposited in GenBank with accession nos. HQ637415–HQ637433 (table 1; appendix).

Sequence Analysis: The sequence data were analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) methods. The MP analyses were conducted using PAUP* 4.0b10 (Swofford, 2003). The branch-and bound search algorithm was used to find the most parsimonious tree(s). Parsimony bootstrap was estimated using the heuristic search method with 1000 replicates.

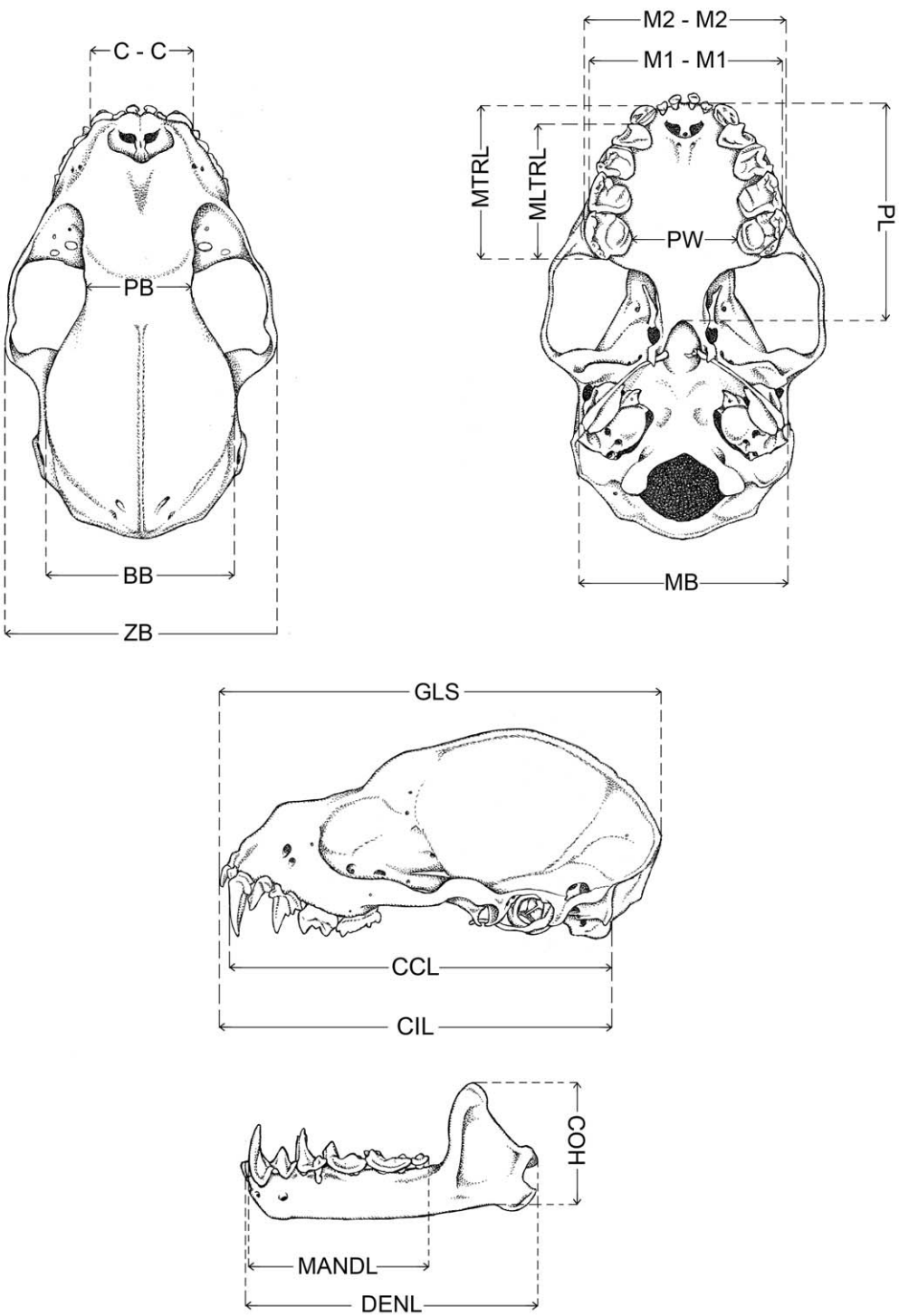

FIGURE 3. Diagram of the cranium of an adult *Vampyrodes caraccioli* showing limits of cranial and dental measurements.

jModelTest version 0.1.1 (Posada, 2008) was used to find the best model for the ML and Bayesian analyses under the Akaike information criterion. The ML analyses were conducted using GARLI 0.96b (Zwickl, 2006) with the following parameters; rate matrix = (2.1162, 10.8217, 2.1162, 1.0000, 23.0589, 1.0000); base frequencies (A = 0.3042, C = 0.2854, G = 0.1317, T = 0.2787); proportion of invariable sites = 0.4650; gamma-distribution shape parameter = 0.5780. Bootstrap support was estimated with 1000 replicates.

Bayesian analyses were conducted using MrBayes version 3.1.2 (Huelsenbeck and Ronquist, 2001) with random starting trees without constraints; four simultaneous Markov chains were run for 10,000,000 generations, with a sampling frequency of 500 steps.

Morphological Analyses

Based on the results of our molecular analyses, museum specimens (appendix) were segregated and analyzed for congruence with patterns detected based on gene sequences. External and osteological characters examined were based on, but not restricted to, those defined by Velazco (2005) and Wetterer et al. (2000). We examined 267 specimens of adult *Vampyrodes* (133 males and 134 females; appendix). We used digital calipers to take 1 external and 20 craniodental measurements to the nearest 0.01 mm on each specimen (fig. 3). Descriptive statistics (mean and observed range) were calculated for all samples.

Forearm length (FA): Distance from the elbow (tip of the olecranon process) to the wrist (including the carpals). This measurement is made with the wing at least partially folded.

Greatest length of skull (GLS): Distance from the posteriormost point on the occiput to the anteriormost point on the premaxilla (including the incisors).

Condyloincisive length (CIL): Distance between a line connecting the posteriormost margins of the occipital condyles and the anteriormost point on the upper incisors.

Condylocanine length (CCL): Distance between a line connecting the posteriormost margins of the occipital condyles and a line connecting the anteriormost surface of the upper canines.

Braincase breadth (BB): Greatest breadth of the globular part of the braincase, excluding mastoid and paraoccipital processes.

Zygomatic breadth (ZB): Greatest breadth across the zygomatic arches.

Postorbital breadth (PB): Least breadth at the postorbital constriction.

Palatal width at canines (C–C): Least width across palate between lingual margins of the alveoli of upper canines.

Mastoid breadth (MB): Greatest breadth across the mastoid region.

Palatal length (PL): Distance between the posterior palatal notch and the anteriormost border of the incisive alveoli.

Maxillary toothrow length (MTRL): Distance from the anteriormost surface of the upper canine to the posteriormost surface of the crown of M3.

Molariform toothrow length (MLTRL): Distance from the anteriormost edge of P3 to the posteriormost edge of the crown of M3.

Width at M1 (M1–M1): Greatest width of palate across labial margins of the alveoli of M1s.
Width at M2 (M2–M2): Greatest width of palate across labial margins of the alveoli of M2s.
Palate width (PW): Greatest width across the inner edges of the crown of M2s.
M1 width (M1W): Greatest width of crown of M1.
M2 width (M2W): Greatest width of crown of M2.
Dentary length (DENL): Distance from midpoint of condyle to the anteriormost point of the dentary.
Mandibular toothrow length (MANDL): Distance from the anteriormost surface of the lower canine to the posteriormost surface of m3.
Coronoid height (COH): Perpendicular height from the ventral margin of mandible to the tip of the coronoid process.
Width of m1 (m1W): Greatest width of crown of m1.

All measurements were log-transformed to achieve normalization for statistical analyses. We evaluated differences between sexes and morphological groups by principal component analysis (PCA) using a correlation matrix. Components with eigenvalues greater than 1 were retained. Principal component (PC) scores were plotted to show relationships between species groups in morphospace. Analyses were performed using SPSS for Windows, version 16.

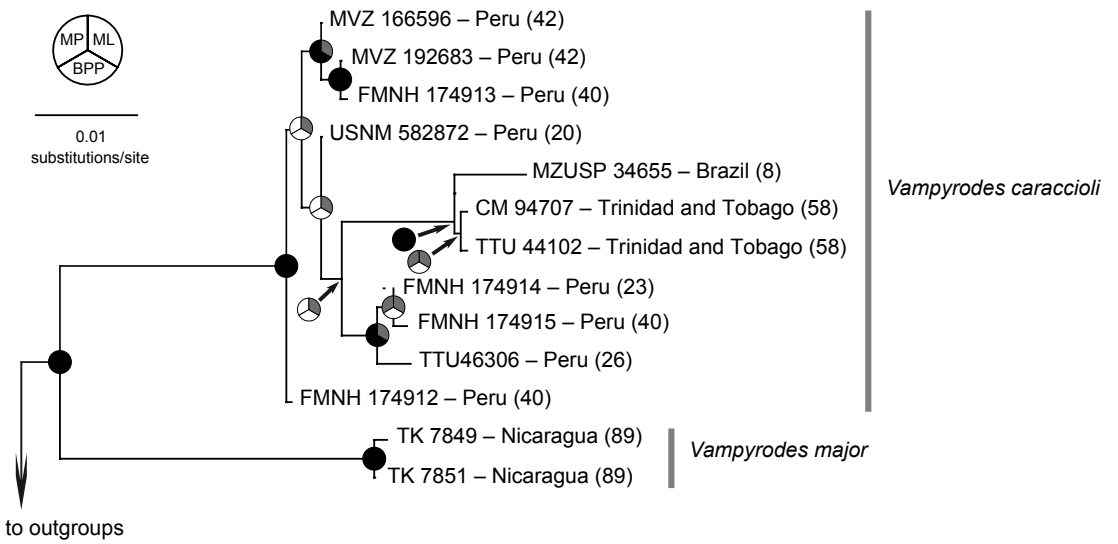

FIGURE 4. Combined cyt-*b* and D-loop maximum likelihood phylogram for both species of *Vampyrodes*. Support statistics from a parsimony bootstrap analysis, a maximum likelihood bootstrap analysis, and a Bayesian analysis are indicated at each resolved node. For the parsimony and maximum likehood analyses (MP and ML, respectively), white indicates bootstrap frequencies ≤50%, grey indicates bootstrap frequencies between 50% and 75%, and black indicates bootstrap frequencies ≥75%. For the Bayesian analysis (BPP), white indicates posterior probabilities <0.95, whereas black indicates posterior probabilities ≥0.95. For each terminal, an alphanumeric identifier and the country of origin (from table 1). Numbers in parentheses refer to localities mapped in figure 6 and listed in the Gazetteer (appendix).

TABLE 2. Pairwise uncorrected percentage of cyt-*b* sequence divergence ($\bar{x}$ ± SE) among *Vampyrodes* and outgroup

	1	2	3	4	5
1 - *Chiroderma villosum*	0				
2 - *Platyrrhinus recifinus*	11.84	0			
3 - *Vampyressa melissa*	12.11	11.05	0		
4 - *Vampyrodes caraccioli*	11.60 ± 0.35	9.80 ± 0.18	11.21 ± 0.29	1.07 ± 0.77	
5 - *Vampyrodes major*	11.67 ± 0.00	10.18 ± 0.00	11.58 ± 0.00	4.96 ± 0.27	0

RESULTS

Molecular Analyses

The combined dataset (1555 bp) included the 16 specimens of *Vampyrodes* and the outgroups. Unweighted MP analysis resulted in two most parsimonious trees (CI = 0.79; tree length = 480). The MP, ML, and BI analyses of the combined cyt-*b* and D-loop recovered *Vampyrodes* as a monophyletic group (fig. 4). The three analyses produced similar topologies and each strongly supported placement of *Platyrrhinus* as the sister group of *Vampyrodes*. All analyses identified two well-supported and reciprocally monophyletic lineages within *Vampyrodes* that correspond to *V. caraccioli* and *V. major*. The mean pairwise distances between cyt-*b* sequences of *V. caraccioli* and *V. major* were over 4.5% (table 2). In the context of genetic distances separating valid species within the sister genus *Platyrrhinus* (Velazco and Patterson, 2008; Velazco et al., 2010b), this value adequately corroborates the distinctiveness of these lineages and supports their recognition as distinct at the species level.

Morphological Analyses

We compared 55 specimens of *V. caraccioli* and 212 of *V. major* using a PCA based on the 21 measurements described earlier. Three different PCAs were performed to explore variation within *Vampyrodes*: (A) an analysis comparing males and females within *V. caraccioli* to investigate possible sexual dimorphism; (B) an analysis comparing males and females within *V. major*; and (C) an analysis comparing *V. caraccioli* with *V. major*. The three analyses extracted five, four, and three components, respectively, that account for 77.9%, 70.0%, and 74.1% of the variation. PCA plots resulting from analyses (A) and (B) showed that males and females in *V. caraccioli* and *V. major* overlap completely (not shown), indicating an absence of sexual dimorphism in both of these species. In the PCA plot from analysis (C), which included all individuals of *V. caraccioli* and *V. major*, individuals of *V. major* fell at the higher end of PC1 (fig. 5A, B). PC1 largely reflects cranial size, and longer and wider skull in *V. major* (table 3). Along PC2 and PC3, these two species overlap, reflecting shape similarities between the two species (fig. 5A, B).

The results of the comparative morphological analyses in which we examined *V. caraccioli* and *V. major* for discretely varying traits in craniodental morphology, pelage, and facial features are included in the diagnoses below.

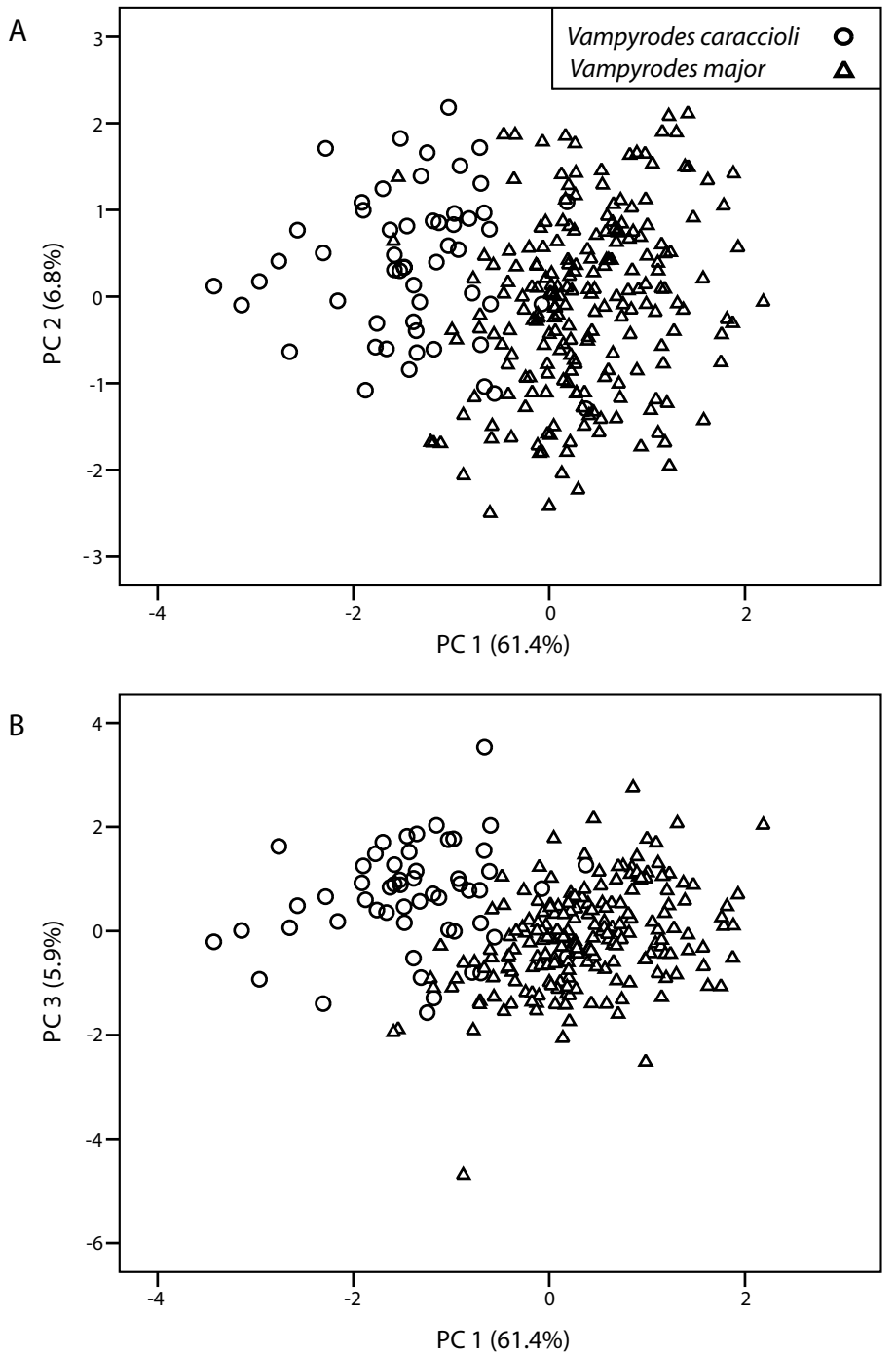

FIGURE 5. Principal components analysis (performed on cranial, dental and one external variables) showing dispersion of scores representing *Vampyrodes caraccioli* (circles) and *V. major* (triangles) along: (A) first and second axes (B) first and third axes. PC1 represents a size axis (with larger specimens appearing toward the right side of the plot) and PC2 portrays a difference in shape.

TABLE 3. Factor loadings for the first three factors extracted from the correlation matrix from a principal component (PC) analysis of 21 variables comparing *Vampyrodes caraccioli* and *Vampyrodes major*

Measurements	PC 1	PC 2	PC 3
GLS	0.92	–0.14	–0.13
CIL	0.92	–0.09	–0.16
CCL	0.92	–0.08	–0.15
BB	0.63	–0.48	–0.02
ZB	0.83	–0.21	0.25
PB	0.68	–0.21	–0.30
C–C	0.75	0.25	0.27
MB	0.83	–0.37	0.00
PL	0.88	–0.04	–0.12
MTRL	0.92	0.19	–0.14
MLTRL	0.87	0.19	–0.15
M1–M1	0.88	0.21	0.19
M2–M2	0.87	0.17	0.31
MXBR	0.55	–0.15	0.66
M1W	0.54	0.58	–0.03
M2W	0.71	0.40	–0.13
DENL	0.90	–0.90	–0.12
MANDL	0.91	0.08	–0.22
COH	0.45	0.13	0.50
m1W	0.78	0.30	–0.12
FA	0.67	–0.27	–0.04
Eigenvalues	13.51	1.51	1.29
Proportion of variation	61.4%	6.8%	5.9%

SYSTEMATICS

FAMILY PHYLLOSTOMIDAE GRAY, 1825

SUBFAMILY STENODERMATINAE GERVAIS, 1856

Vampyrodes Thomas, 1900

Vampyrops: Thomas, 1889: 167; part; not *Vampyrops* Peters, 1865.

Vampyrodes Thomas, 1900: 270; type species *Vampyrops caraccioli* Thomas, 1889, by original designation; described as a subgenus of *Vampyrops* Peters.

Distribution: *Vampyrodes* is known from southern Mexico southward to Colombia, Venezuela, Guyana, Suriname, French Guiana, Trinidad and Tobago, northern, eastern, and western Brazil, Ecuador, eastern Peru, and northern Bolivia (fig. 6).

Emended Diagnosis: *Vampyrodes* is a genus of medium to large-sized fruit-eating bats (FA 47.3–58.6 mm, GLS 25.1–29.1 mm, CCL 22.0–25.7 mm; tables 4–5). Dorsal fur pale brown to dark brown, with individual hairs bicolored with pale base and darker tip; ventral fur slightly grayer than dorsal fur, with individual hairs tricolored, with a basal pale brownish band that makes up some 70% to 80% of the total length of each hair, a short dark brown (~ 10% of the total length of each hair) subterminal band, and a tiny pale brownish terminal band; dorsal stripe brilliant white and wide; conspicuous facials stripes, supraorbital facial stripes extend from the lateral margin of the noseleaf to the top of the head between the ears, malar stripes extend from the corner of the mouth to the base of the ears; folds in the pinnae are not well marked but are distinguishable; enamel surface of the upper and lower dentition with periky-

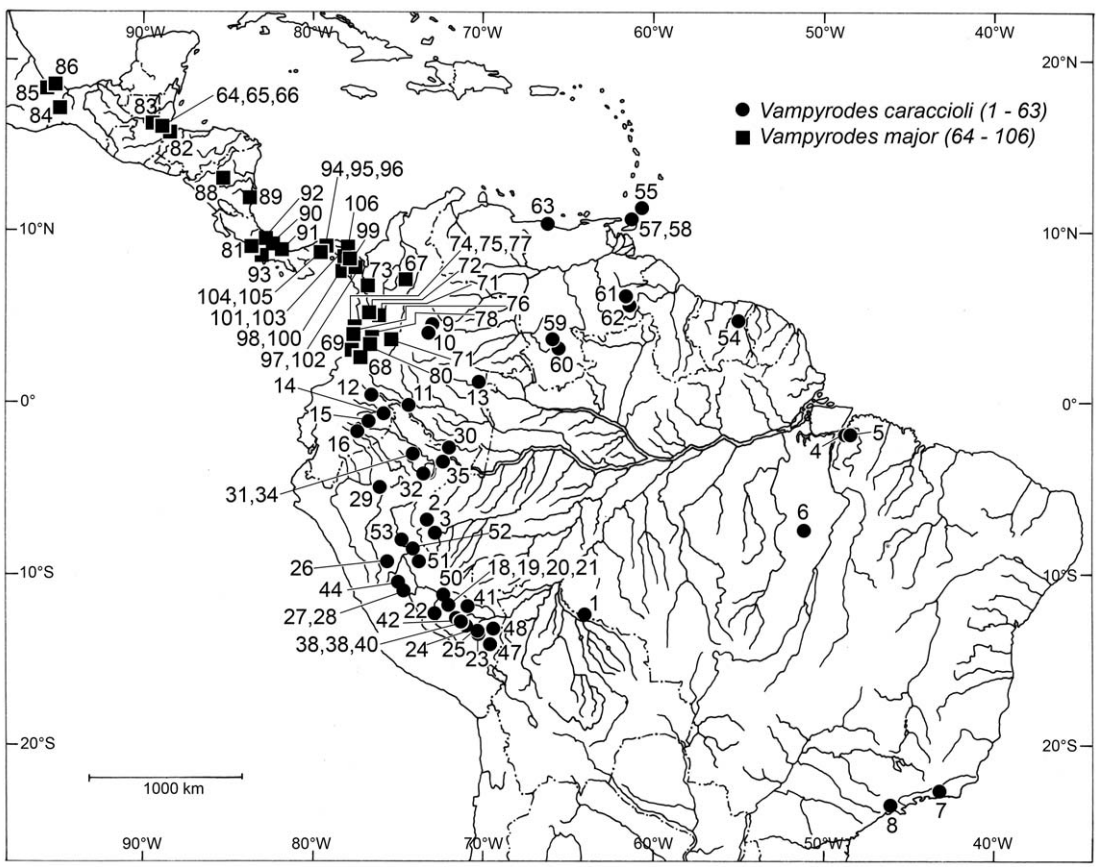

FIGURE 6. Map showing collecting localities of *Vampyrodes caraccioli* (circles) and *V. major* (squares). Numbers refer to entries in the Gazetteer (appendix).

TABLE 4. Measurements (mm) and sample statistics[a] of *Vampyrodes caraccioli*

	BMNH 89.6.10.2[b]	BMNH 24.3.1.63[c]	Adult females	Adult males
FA	49.70	53.45	52.80 ± 1.75 (47.28–55.98) 27	51.91 ± 1.40 (48.79–53.96) 19
GLS	–	26.50	26.61 ± 0.55 (25.22–27.97) 31	26.38 ± 0.61 (25.14–27.56) 24
CIL	–	24.75	24.07 ± 0.64 (22.54–25.40) 31	24.02 ± 0.63 (22.99–25.34) 24
CCL	–	23.90	23.49 ± 0.63 (21.98–24.98) 31	23.42 ± 0.58 (22.58–24.66) 24
BB	–	11.30	11.40 ± 0.28 (10.88–11.91) 31	11.49 ± 0.30 (10.90–11.94) 24
ZB	–	16.65	16.97 ± 0.50 (15.92–17.89) 31	16.79 ± 0.43 (15.76–17.62) 24
PB	6.10	6.30	6.36 ± 0.21 (5.87–6.79) 31	6.33 ± 0.18 (5.99–6.69) 24
C–C	6.30	6.90	6.76 ± 0.21 (6.13–7.08) 31	6.73 ± 0.16 (6.26–6.96) 24
MB	–	12.50	12.34 ± 0.32 (11.78–13.24) 31	12.27 ± 0.26 (11.57–12.80) 24
PL	12.45	13.25	13.63 ± 0.51 (12.25–14.39) 31	13.64 ± 0.44 (12.99–14.46) 24
MTRL	9.50	10.10	9.75 ± 0.25 (9.23–10.25) 31	9.65 ± 0.19 (9.34–9.94) 24
MLTRL	7.85	8.30	8.14 ± 0.25 (7.71–8.77) 31	8.00 ± 0.22 (7.55–8.43) 24
M1–M1	11.00	11.65	11.61 ± 0.32 (10.78–12.28) 31	11.50 ± 0.35 (10.64–12.22) 24
M2–M2	11.20	11.80	11.94 ± 0.28 (11.23–12.37) 31	11.84 ± 0.33 (11.17–12.37) 24
MXBR	6.30	6.25	6.39 ± 0.23 (6.02–7.08) 31	6.27 ± 0.18 (5.93–6.64) 24
M1W	2.70	3.35	2.87 ± 0.13 (2.58–3.11) 31	2.89 ± 0.15 (2.55–3.12) 24
M2W	2.85	3.00	3.22 ± 0.12 (2.97–3.41) 31	3.20 ± 0.09 (3.01–3.40) 24
DENL	17.35	18.10	17.91 ± 0.44 (16.91–19.10) 29	17.88 ± 0.46 (17.12–19.07) 24
MANDL	10.50	–	10.71 ± 0.28 (10.04–11.27) 29	10.63 ± 0.36 (10.06–11.27) 24
COH	7.45	7.50	7.80 ± 0.31 (7.13–8.28) 29	7.67 ± 0.23 (7.28–8.23) 24
m1W	1.90	1.85	1.94 ± 0.09 (1.76–2.11) 29	1.92 ± 0.07 (1.76–2.05) 24

[a] The sample mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size are provided for each sex.
[b] Holotype of *V. caraccioli*, a subadult of unknown sex.
[c] Holotype of *V. ornatus*, an adult female.

mata (fig. 7, top); sulcus mesial to P4 absent; lingual cingulae absent at the bases of the metacones of M1 and M2; M3 absent; p4 lingual accessory cuspule present; lingual cingulid absent on m1; stylid cusp mesial of the protoconid of m1 absent.

Vampyrodes is easily distinguished from *Chiroderma* by the presence of nasal bones (absent in *Chiroderma*) and mesiodistally broad and buccolingually compressed upper incisors (slender and pointed in *Chiroderma*); from *Platyrrhinus* and *Uroderma* by the absence of M3 (present in *Platyrrhinus and Uroderma*); and from *Vampyressa* and *Vampyriscus* by its greater skull length (shorter in *Vampyressa* and *Vampyriscus*: GLS < 24 mm).

Remarks: Perikymata or "waves around the tooth" seen on some mammalian teeth are transverse lines on the enamel that are external manifestations of incremental lines of Retzius (Moss-Salentijn et al., 1997). Perikymata present in *Vampyrodes* can be directly observed with the aid of a dissecting scope as long they have not been completely eroded by tooth wear. Poorly developed perikymata can be observed in species of *Artibeus* (*A. jamaicensis:* AMNH 177758; *A. lituratus:* AMNH 260239) and *Dermanura* (*D. anderseni:* AMNH 210822; *D. cinerea:* AMNH 29689; *D. glauca:* AMNH 24393). Perikymata have been reported in Artiodactyla (Kierdorf et al., 2000), Carnivora (present in Hyaenidae [Ferretti, 2007] but absent in *Canis* and *Felis* [Skobe et al., 1985]), †Notoungulata (Gelfo et al., 2008), Perissodactyla (Hillson, 2005; von Koenigswald et al., 2011), most Primates (including fossil and recent Hominidae; Beynon and Wood, 1987; Maas and Dumont, 1999; Guatelli-Steinberg et al., 2004), Proboscidea (Ferretti, 2008), and some Rodentia (Flynn and Morgan, 2005). This is the first record of perikymata in Chiroptera to our knowledge (Lester and Hand, 1987; Lester et al., 1988).

Vampyrodes caraccioli (Thomas, 1889)

Caracciolo's Stripe-faced Bat

Figures 1, 2, 8, 9, and 10

Vampyrops Caracciolæ Thomas, 1889: 167; type locality "Trinidad."

Vampyrops Caraccioli Thomas, 1893a: 186; corrected original spelling.

V[*ampyrops*. (*Vampyrodes*)] *Caraccioli*: Thomas, 1900: 270; name combination.

Vampyrodes caracciolæ: Miller, 1907: 156; first use of current name combination and incorrect subsequent spelling of *Vampyrops caraccioloi* Thomas.

Vampyrodes ornatus Thomas, 1924: 532; type locality "San Lorenzo, Rio Marañon, nearly opposite mouth of Huallaga. Alt. 500′," Loreto, Peru.

V[*ampyrodes*]. *caraccioloi* Pittier and Tate, 1932: 273; incorrect subsequent spelling of *Vampyrodes caraccioli* Thomas.

Vampyrodes caraccioloi Goodwin and Greenhall, 1961: 257; unjustified emendation of *Vampyrops caraccioli* Thomas.

Vampyrodes ornata Goodwin and Greenhall, 1961: 257; incorrect subsequent spelling of *Vampyrodes ornatus* Thomas.

Type Material: The holotype of *V. caraccioli* is BMNH 89.6.10.2, a subadult of undetermined sex prepared as a skin and skull. The skin is in good condition, but the skull is damaged.

The braincase was removed, a distal section of the parietals are missing, and there is a hole on the right parietal. The occipital bone is mostly missing, although the proximal section of the basioccipital is present; the left squamosal and zygomatic arch are missing. The mandibles are intact but were separated at some point and glued together afterward. *V. caraccioli* was collected by Henry Caracciolo in Trinidad at an unspecified locality.

Distribution: *Vampyrodes caraccioli* is known from eastern Colombia, eastern Ecuador, Peru, northern Bolivia, Venezuela, Trinidad and Tobago, French Guiana, Guyana, Suriname, and Brazil (fig. 6).

Emended Diagnosis: Dorsal fur pale brown to dark brown, 7–9 mm long; two genal vibrissae present; uropatagium with inverted U-shaped posterior margin fringed with short (< 2 mm) dense hair along its free edge; metacarpal III longer than metacarpal V; rostrum slender; well-developed anterior notch present in nasals; parietal foramina well separated from nuchal crest; weakly developed groove present between occipital condyle and paracondylar process; paraoccipital processes well developed; perikymata present on all upper and lower teeth; I1 broad and bilobed but appears single lobed in older individuals with worn teeth; M1 postentoconule absent or poorly developed; M2 parastyle absent or poorly developed; M2 postentoconule absent or weakly developed; lower incisors robust and bilobed; lingual accessory cuspule present on p4; cuspule on m1 and m2 paracristid absent.

Description and Comparisons: A medium-sized *Vampyrodes* (FA 47.28–55.98 mm; GLS 25.14–27.97 mm; CCL 21.98–24.98 mm; table 4). All linear measurements of *V. caraccioli* show a slight overlap with those of *V. major,* with *V. caraccioli* being the smaller of the two species (tables 4–5). Dorsal pelage in *V. caraccioli* is long (7–9 mm) and brown, with individual hairs bicolored with darker tips. Compared with *V. major*, the pelage tends to be slightly lighter and the hairs shorter (9–10 mm in *V. major*). The ventral pelage is similar but slightly darker, with individual hairs tricolored, with a basal pale brownish band that makes up some 70% to 80% of the total length of each hair. Each hair also has a short dark brown (~ 10% of the total length of each hair) subterminal band, and a tiny pale brownish terminal band. The uropatagium in *V. caraccioli* has an inverted U-shaped posterior margin with dense and short hair (< 2 mm) along the trailing edge (V-shaped posterior margin in *V. major* with dense and long hair (> 2 mm) along the trailing edge). The width of uropatagium in *V. caraccioli* is 5–9 mm at midline (6–10 mm in *V. major*). The proximal half of forearm is covered with dense, short hair. Metacarpal III is longer than metacarpal V in *V. caraccioli* (the metacarpal III is shorter than metacarpal V in *V. major*). The plagiopatagium inserts onto the tarsal bones. Two genal vibrissae are present in *V. caraccioli* (three genal vibrissae are present in *V. major*). *V. caraccioli* has six vibrissae surrounding the margin of the noseleaf in a single array; two vibrissae on each side of upper lip below the vibrissae surrounding the noseleaf; four submental vibrissae on each side of chin; and two interramal vibrissae. The noseleaf is longer than it is wide and the inferior border of the nasal horseshoe is completely free of upper lip.

The skull of *V. caraccioli* has a slender rostrum (broad and robust in *V. major*) and a well-developed anterior notch in the nasals (absent or weakly developed in *V. major*). Two infraor-

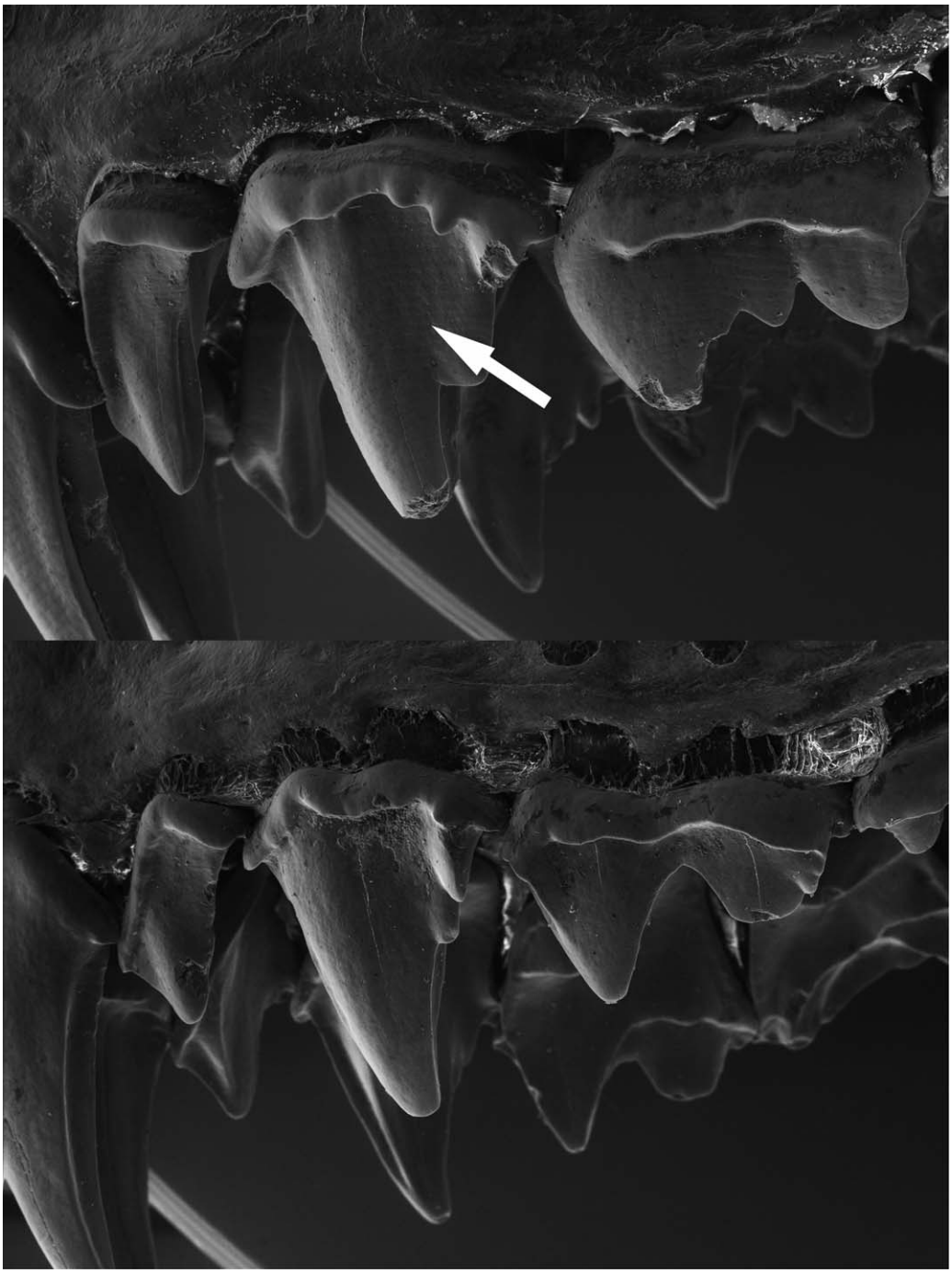

FIGURE 7. Labial view of the left P3–M1 illustrating presence and absence of perikymata. **Top**, *Vampyrodes caraccioli* (AMNH 230653) with distinct perikymata (arrow). **Bottom**, *Platyrrhinus lineatus* (AMNH 23771) without distinct perikyma.

bital foramina usually present (three infraorbital foramina are present on one specimen examined: USNM 405129). The parietal foramina are well separated from the nuchal crest in *V. caraccioli* (USNM 405129; figs. 8A, 10A) whereas in *V. major* (FMNH 127114; figs. 8C, 10B) these foramina are closer to the nuchal crest. The groove between the occipital condyle and paracondylar process is weakly developed (USNM 405129; FMNH 139776; fig. 10A). Compared with *V. major*, the groove between the occipital condyle and paracondylar process is well developed (FMNH 58263; fig. 10B). The paraoccipital processes are well developed (moderately developed in *V. major*).

Perikymata are present on all upper and lower teeth (fig. 7, top). The upper inner incisors are broad; both the outer and inner incisors are bilobate (USNM 361711), but may appear single lobed in older individuals with worn teeth (USNM 528341). By comparison, in *V. major* the upper inner incisors are slender. P3 is more than half the size of P4 in *V. caraccioli*, and two stylar cuspules are present on posterior cristid of P4. The M1 lacks a parastyle but both a mesostyle and metastyle are present, and a stylar cuspule is present on the labial cingulum of the metacone. A sulcus is present on the posterior cristid of the M1 paracone, the protocone is well developed, and a postentoconule is absent or poorly developed on M1. On M2 the parastyle is absent or poorly developed (FMNH 139776) (well developed in *V. major*), the labial cingulum on the paracone is absent or poorly developed, and the postentoconule is absent or poorly developed (well developed in *V. major*). The lower incisors are robust and bilobed (small in *V. major*). A p4 lingual accessory cuspule is present. A cuspule on the m1 paracristid is absent in *V. caraccioli* (present in *V. major*). A cuspule on the m2 paracristid is always absent in *V. caraccioli*. In *V. major*, this cuspule is sometimes present (AMNH 186381) and sometimes absent (USNM 314717).

Natural History: *Vampyrodes caraccioli* is a frugivorous bat that has been reported to feed on at least six plant species representing three genera in two families: *Spondias mombin* (Anacardiaceae) and *Ficus insipida*, *F. obtusifolia*, *F. yoponensis*, *F.* sp, and *Poulsenia armata* (Moraceae) (Foster et al., 1986; Kalko and Handley, 2001; Lobova et al., 2009). Lobova et al. (2009) reported an epizoochorous dispersal by *V. caraccioli* of *Cyathula prostrata* (Amaranthaceae), a terrestrial herb with diaspores that adhere to the fur of its dispersal agents.

Very few reports of roosts of *Vampyrodes caraccioli* have been published. Day roosts include foliage, branches, and palm fronds where groups of two to four have been recorded (Husson, 1954; Goodwin and Greenhall, 1961).

Two species of ectoparasite (*Periglischrus iheringi:* Spinturnicidae; *Speleochir brasiliensis:* Ereynetidae) have been reported from *V. caraccioli* from a Brazilian specimen (Confalonieri, 1976; Fain and Aitken, 1969) and one from a Venezuelan specimen (*Paratrichobius* sp., *salvini* complex: Streblidae) (Wenzel, 1976). Nogueira et al. (2004) reported that 66% of *V. caraccioli* captured in western Amazonia of Brazil were infested with trematode *Hasstilesia tricolor* in their small intestines.

Like other stenodermatines, *Vampyrodes caraccioli* has a litter size of one (Tuttle, 1970; Graham, 1987). Reproductive data suggest possible seasonal polyestry; pregnant females have

TABLE 5. Measurements (mm) and sample statistics[a] of *Vampyrodes major*

	MCZ 6756[b]	Adult females	Adult males
FA	55.35	55.11 ± 1.23 (52.06–58.64) 103	54.19 ± 1.21 (51.36–56.93) 109
GLS	27.74	27.88 ± 0.49 (26.65–28.96) 102	27.66 ± 0.48 (26.26–29.06) 109
CIL	25.61	25.25 ± 0.44 (23.88–26.14) 101	25.07 ± 0.49 (23.71–26.52) 109
CCL	24.80	24.62 ± 0.43 (23.39–25.53) 102	24.41 ± 0.48 (23.09–25.71) 109
BB	12.00	11.90 ± 0.28 (11.24–12.70) 102	11.89 ± 0.29 (11.09–12.65) 109
ZB	18.36	17.56 ± 0.33 (16.87–18.48) 103	17.40 ± 0.37 (16.33–18.47) 109
PB	7.14	6.70 ± 0.21 (6.20–7.35) 103	6.72 ± 0.19 (6.33–7.28) 109
C–C	7.00	7.02 ± 0.21 (6.58–7.67) 103	6.95 ± 0.23 (6.35–7.47) 109
MB	13.23	12.89 ± 0.23 (12.33–13.53) 103	12.83 ± 0.25 (12.20–13.63) 109
PL	14.25	14.50 ± 0.36 (13.68–15.51) 103	14.39 ± 0.36 (13.54–15.44) 109
MTRL	10.43	10.31 ± 0.23 (9.78–10.91) 103	10.23 ± 0.25 (9.68–10.78) 109
MLTRL	8.50	8.57 ± 0.20 (8.14–9.07) 103	8.49 ± 0.22 (7.98–9.04) 109
M1–M1	12.63	12.19 ± 0.30 (11.60–12.94) 103	12.03 ± 0.33 (10.97–12.79) 109
M2–M2	12.58	12.44 ± 0.29 (11.93–13.32) 103	12.30 ± 0.34 (10.95–13.14) 109
MXBR	6.86	6.51 ± 0.21 (6.06–7.05) 103	6.42 ± 0.25 (5.46–6.97) 109
M1W	2.90	2.99 ± 0.16 (2.58–3.37) 103	2.98 ± 0.15 (2.59–3.30) 109
M2W	3.20	3.35 ± 0.12 (3.00–3.74) 103	3.34 ± 0.12 (3.05–3.60) 109
DENL	19.38	19.08 ± 0.36 (18.28–19.81) 102	18.88 ± 0.41 (17.49–19.89) 109
MANDL	11.44	11.56 ± 0.23 (11.07–12.14) 102	11.46 ± 0.26 (10.86–12.06) 109
COH	7.42	7.87 ± 0.28 (7.27–8.55) 102	7.71 ± 0.29 (6.90–8.41) 109
m1W	2.07	2.06 ± 0.08 (1.90–2.28) 102	2.04 ± 0.08 (1.79–2.30) 109

[a] The sample mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size are provided for each sex.
[b] Holotype of *V. major*, an adult female.

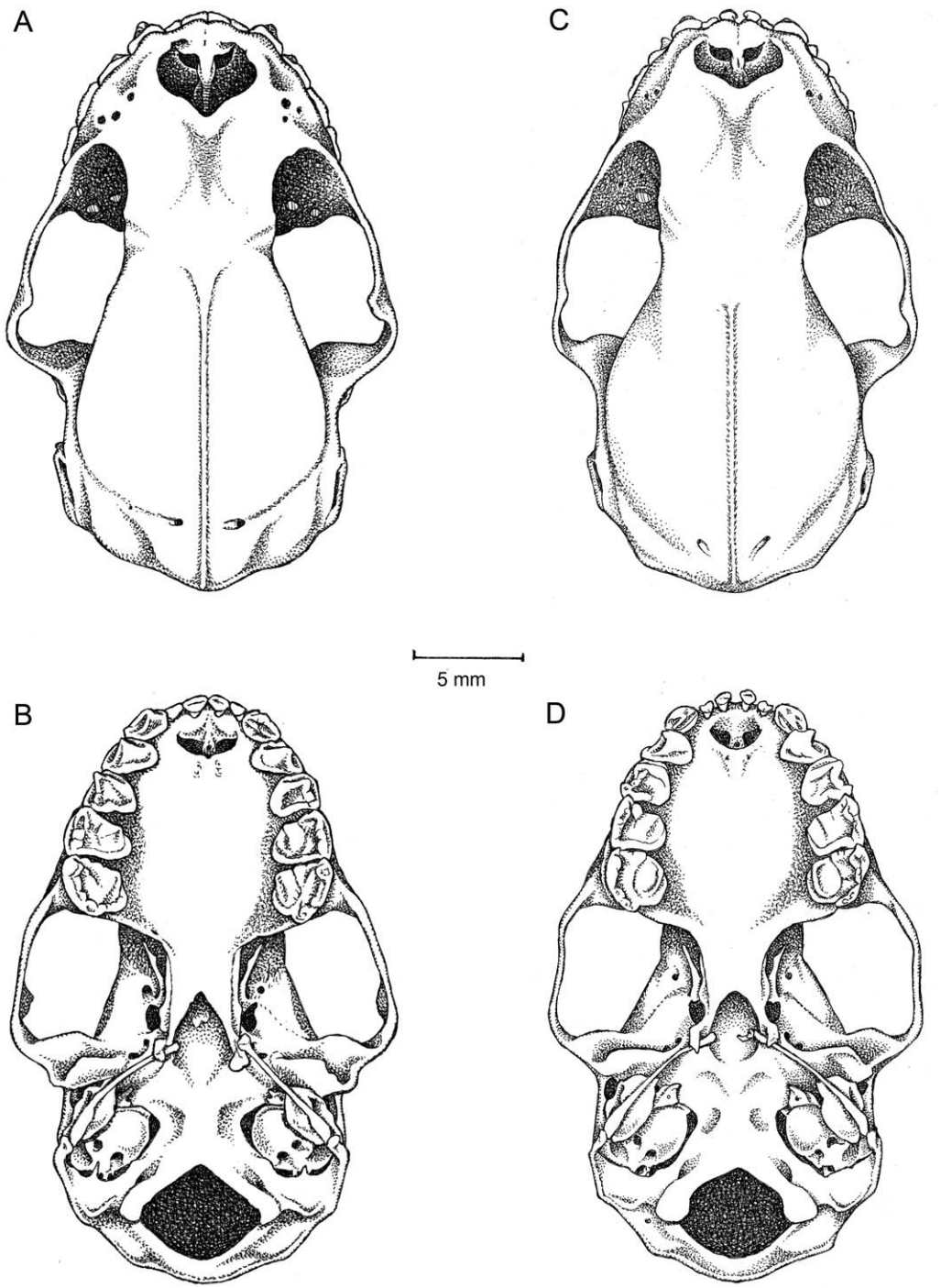

FIGURE 8. Dorsal (**A**) and ventral (**B**) views of the skull of *Vampyrodes caraccioli* (USNM 405129; male) from Amazonas, Venezuela; the stylohyals were reconstructed from USNM 582872, a female from Cuzco, Peru. Dorsal (**C**) and ventral (**D**) views of the skull of *V. major* (FMNH 127114; male) from Veracruz, Mexico.

been captured in July, September, October, November, December, and January (Tuttle, 1970; Davis and Dixon, 1976; Graham, 1987; Moya and Arteaga, 2007). Lactating females have been captured in October (Moya and Arteaga, 2007).

Karyology: *Vampyrodes caraccioli* has a diploid chromosome number (2*n*) of 30 and a fundamental number (FN) of 56. The X chromosome is subtelocentric and the Y chromosome is submetacentric (Baker and Hsu, 1970; Baker, 1973).

Remarks: The holotype of *Vampyrodes ornatus* BMNH 24.3.1.63, is an adult female with a hole on the right parietal, missing the right tympanic bula and both m3. Measurements of this holotype are shown in table 4. Forman and Genoways (1979) reported that the head morphology of the sperm of *V. caraccioli* is unique in being long and having an unusually narrow apex and base.

Vampyrodes major Allen, 1908

Great Stripe-faced Bat

Figures 8–10

Vampyrodes major Allen, 1908: 38; type locality "San Pablo, Isthmus of Panama," Canal Zone, Panama.

Type Material: The holotype MCZ 6756, an adult female, preserved in alcohol with the skull removed and cleaned, was collected by Allen Lesley at San Pablo, Isthmus of Panama, Canal Zone, Panama. The body and skull are in good condition. The type locality is now covered by the waters of Gatún Lake (Goldman, 1920).

Distribution: *Vampyrodes major* is known from southern Mexico (Chiapas and Oaxaca), Belize, Guatemala, Honduras, Nicaragua, Honduras, Costa Rica, Panama, western Colombia and Ecuador (fig. 6). *V. major* is expected to occur in El Salvador, but has not been reported yet (Burt and Stirton, 1961; Owen et al., 1991).

Emended Diagnosis: Dorsal fur is dark brown, 9–10 mm long; three genal vibrissae present; inverted V-shaped posterior margin of the uropatagium; uropatagium fringed with long (> 2 mm), dense hair along trailing edge; metacarpal III shorter than metacarpal V; rostrum broad and robust; parietal foramina close to nuchal crest; absent or weakly developed anterior notch in the nasals; well-developed groove present between the occipital condyle and paracondylar process; paraoccipital processes moderately developed; perikymata present on all upper and lower teeth; I1 slender and bilobed but appears single lobed in older individuals with worn teeth; M1 postentoconule absent or poorly developed; M2 parastyle well developed; M2 postentoconule well developed; lower incisors small and bilobed; lingual accessory cuspule present on p4; cuspule on m1 paracristid present; cuspule on m2 paracristid sometimes present and sometime absent.

Description and Comparisons: A medium-sized *Vampyrodes* (FA 51.36–58.64 mm; GLS 26.26–29.06 mm; CCL 23.09–25.71 mm; table 5). All linear measurements of *V. major* show a small overlap with those of *V. caraccioli* with *V. major* being the larger of the two species (tables

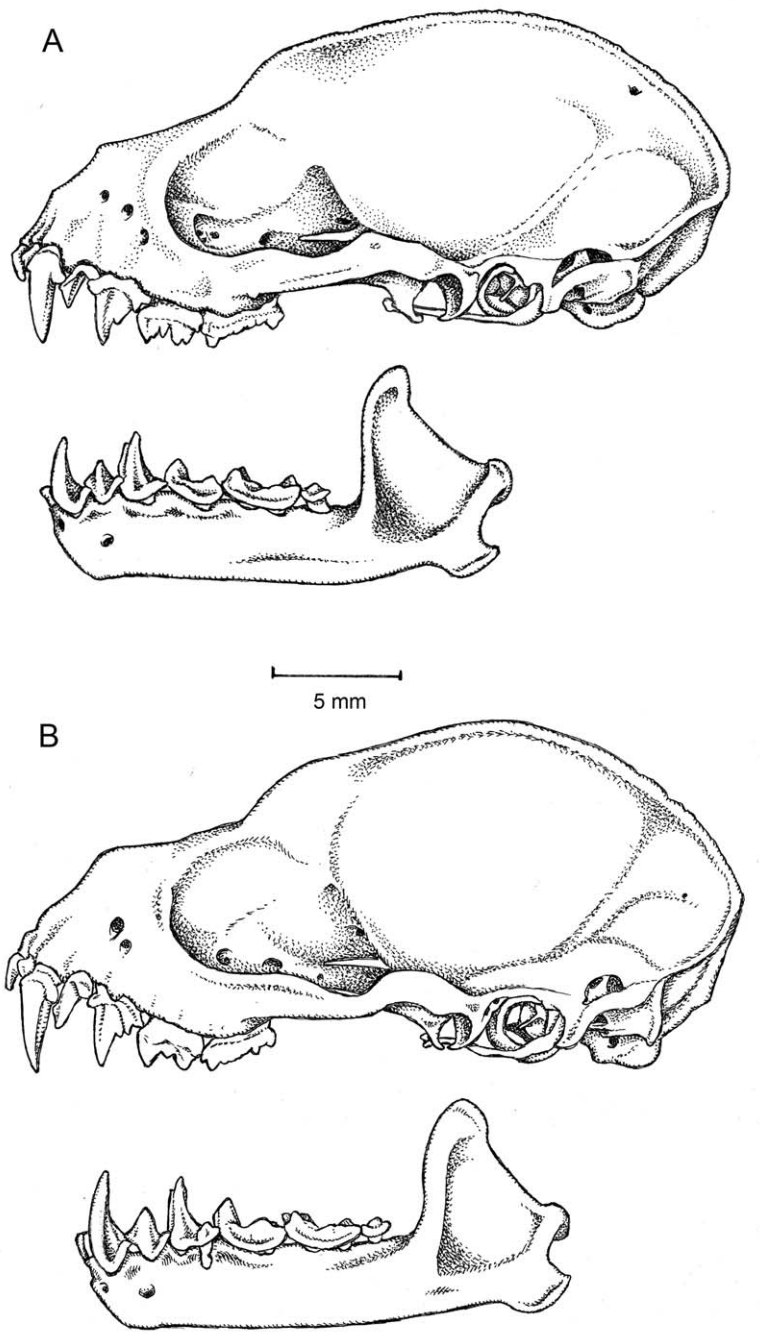

FIGURE 9. Lateral views of the skulls and lower jaw of (**A**) *Vampyrodes caraccioli* (USNM 405129; male); the stylohyal was reconstructed from USNM 582872. Lateral views of the skulls and lower jaw of (**B**) *V. major* (FMNH 127114; male).

4–5). The dorsal pelage in *V. major* is long (9–10 mm) and brown, with individual hairs bicolored with darker tips. Compared with *V. caraccioli*, the pelage tends to slightly darker and the hairs longer (7–9 mm in *V. caraccioli*). The ventral pelage is similar but slighty darker than in the latter species, with individuals hairs tricolored, with a basal pale brownish band that makes up some 70% to 80% of the total length of each hair, a short dark brown (~ 10% of the total length of each hair) subterminal band, and a tiny pale brownish terminal band. The uropatagium in *V. major* has an inverted V-shaped posterior margin with dense and long hair (> 2 mm) along the trailing edge (U-shaped posterior margin, with dense and short hair (< 2 mm) along the trailing edge in *V. caraccioli*). The width of uropatagium in *V. major* is 6–10 mm long at midline (in *V. caraccioli* the uropatagium tends to be slightly shorter, 5–9 mm). The proximal half of forearm in *V. major* is covered with dense, short hair. Metacarpal III is shorter than metacarpal V in *V. major* (metacarpal III is longer than metacarpal V in *V. caraccioli*). The plagiopatagium inserts onto the tarsal bones in both species. Three genal vibrissae are present in *V. major* (two genal vibrissae are present in *V. caraccioli*). *V. major* has six vibrissae surrounding the margin of the noseleaf in a single array; two vibrissae on each side of upper lip below the vibrissae surrounding the noseleaf; four submental vibrissae on each side of chin; two interramal vibrissae. The noseleaf is longer than wide and the inferior border of nasal horseshoe is completely free of upper lip.

The skull of *V. major* has a broad and robust rostrum (slender in *V. caraccioli*) and the anterior notch in the nasals is absent or weakly developed (well developed in *V. caraccioli*). Two infraorbital foramina are usually present (multiple infraorbital foramina [> 4] are present on one specimen examined: USNM 309833). The parietal foramina are close to the nuchal crest (FMNH 127114; fig. 10B), whereas they are located much further from the nuchal crest in *V. caraccioli* (USNM 405129; fig. 10A). The groove between the occipital condyle and paracondylar process is well developed (FMNH 58263; fig. 10B); in comparison, in *V. caraccioli* the groove between the occipital condyle and paracondylar process is weakly developed (USNM 405129; FMNH 139776; fig. 10A). The paraoccipital processes are moderately developed in *V. major* (well developed in *V. caraccioli*).

Perikymata are present in all upper and lower teeth in *V. major*. The upper inner incisors are slender; both outer and inner incisors are bilobate (FMNH 127114; USNM 539812), but appear single lobed in older individuals with worn teeth (AMNH 186381). Within comparison, in *V. caraccioli*, the upper inner incisors are mesiodistally broad. P3 is more than half the size of P4, and there are two stylar cuspules present on posterior cristid of P4 in *V. major*. The M1 parastyle is absent, but both a mesostyle and metastyle are present, and a stylar cuspule is present on the labial cingulum of the M1 metacone. A sulcus is present on the posterior cristid of the M1 paracone, the protocone is well developed, and the postentoconule is absent or poorly developed on M1. On M2 the parastyle is well developed (FMNH 127114) (absent or poorly developed in *V. caraccioli*), the labial cingulum on the paracone is absent or poorly developed, and the postentoconule is well developed (absent or poorly developed in *V. caraccioli*). The lower incisors are small and bilobed (robust and bilobed in *V. caraccioli*). A p4 lingual accessory cuspule is present. A cuspule on the m1 paracristid is present in *V. major* (absent in *V.*

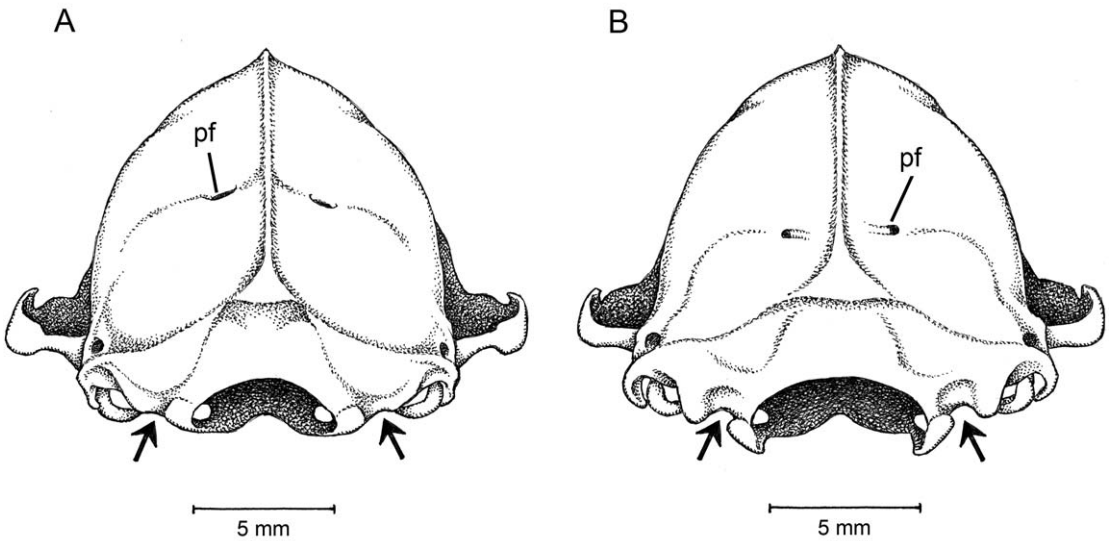

FIGURE 10. Posterior views of the occipital region in *Vampyrodes caraccioli* (**A,** USNM 405129) and *V. major* (**B,** FMNH 127114) illustrating taxonomic differences in the groove between the occipital condyle and the paracondylar process (arrow) and the position of the parietal foramina (**pf**). In *V. caraccioli* the groove between the occipital condyle and paracondylar process is weakly developed and the pf are well separated from the nuchal crest. In *V. major*, however the groove between the occipital condyle and the paracondylar process is well developed and the pf are closer to the nuchal crest.

caraccioli). A cuspule on the m2 paracristid is sometimes present (AMNH 186381) and sometimes absent (USNM 314717) in *V. major*. In *V. caraccioli*, this cuspule is always absent.

Natural History: The natural history of *Vampyrodes major* has been extensively studied (under the name *V. caraccioli*) Barro Colorado Island, Panama (Bonaccorso, 1979; Giannini and Kalko, 2004). *V. major* is a frugivorous bat that has been reported to take fruits/infrutescences of 13 species representing five genera in four families: *Spondias mombin*, *Spondias radlkoferi* (Anacardiaceae); *Calophyllum longifolium* (Clusiaceae); *Ficus dugandii*, *F. insipida*, *F. maxima*, *F. obtusifolia*, *F. pertusa*, *F. trigonata*, *F. yoponensis*, *F.* sp. and *Poulsenia armata* (Moraceae), and *Piper* sp. (Piperaceae) (Bonaccorso, 1979; Morrison, 1980; Handley et al., 1991; Kalko et al., 1996; Medellín and Gaona, 1999; Wendeln et al., 2000; Giannini and Kalko, 2004).

Four species of ectoparasites have been obtained from Panamanian specimens of *Vampyrodes major: Chirnyssoides caparti* (Sarcoptidae), *Parichoronyssus* sp. (Macronyssidae), *Strebla vespertilionis* (Streblidae), and *Periglischrus iheringi* (Spinturnicidae) (Furman, 1966; Wenzel et al., 1966).

Like *Vampyrodes caraccioli*, *V. major* has a litter size of one (Davis et al., 1964; Jones, 1964; Jones et al., 1971). Reproductive data suggested seasonal polyestry; pregnant females have been captured in all months but in December (Davis et al., 1964; Jones, 1964; Jones et al., 1971; Valdez and LaVal, 1971; Fleming et al., 1972; Thomas, 1972; Bonaccorso, 1979; Estrada and Coates-Estrada, 2001). Lactating females have been captured from January to September (Davis et al., 1964; Thomas, 1972; Bonaccorso, 1979).

Karyology: *Vampyrodes major* has a similar karyotype of *V. caraccioli* ($2n = 30$, FN = 56). The X chromosome is subtelocentric and the Y chromosome is submetacentric (Baker, 1973).

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APPENDIX

Specimens Examined

The following list includes all the specimens used in this study, with their respective localities. See Material and Methods for abbreviations. Individuals or series marked with an asterisk were used in the elaboration of tables 3–5 and in the morphometric analyses. Individuals in bold were used in the molecular analyses.

Vampyrodes caraccioli (total 213)

BOLIVIA (total 1)

1. *Beni*, Curiche River mouth (12°40′S, 63°30′W), AMNH 209518*.

BRAZIL (total 32)

2. *Acre*, Foot of the Serra da Jaquirana, Parque Nacional da Serra do Divisor (7°27′S, 73°41′W), ALP 7089, 7094, 7102.3.
3. *Acre*, 30 km E of Cruzeiro do Sul, Rio Juruá, Seringal Lagoinha (07°40′S, 72°40′W), DZSJRP 13028.
4. *Pará*, Belem (1°26′S, 48°28′W), USNM 361711*, 390516, 460122*; Fazenda Velha, Belem, [= Belem; same coordinates], USNM 361712*.
5. *Pará*, Mocambo, Belem (01°27′S, 48°30′W), USNM 393019–393024*, 460114–460121*, 460123*; Utinga, Belem [= Mocambo, Belem; same coordinates], FMNH 126598–126599).
6. *Pará*, Área Indígena Kayapó, Ourilândia do Norte (7°41′S, 51°52′W), MZUSP 29149, 34709–34711.
7. *Rio de Janeiro*, Rio de Janeiro (22°54′S, 43°14′W), MN 43101–43102.
8. *São Paulo*, Núcleo São Sebastião, Parque Estadual da Serra do Mar (23°43′S, 45°45′W), **MZUSP 34655**.

COLOMBIA (total 7)

9. *Meta*, Acacias (3°46′N, 73°50′W), USNM 597083–597084
10. *Meta*, Finca La Reforma, Aguas Claras, Cubarral (3°59′N, 73°45′W), ICN 13820.
11. *Putumayo*, Caño Caucaya Limoncocha, Puerto Leguizamo (0°12S, 74°46W), IAvH-M 593.
12. *Putumayo*, Rio Guamues, San Antonio (0°31′N, 76°45′W), FMNH 113948.
13. *Vaupes*, Mitu (01°08′N, 70°03′W), USNM 445471–445472.

ECUADOR (total 6)

14. *Napo*, Limoncocha (0°25′S, 76°04′W), USNM 528341–528342*.
15. *Pastaza*, Arajuno (1°14′S, 77°41′W), USNM 548398*.
16. *Pastaza*, 130 km S of Coca, Tiguino (1°07′S, 76°57′W), USNM 574536*, 574638.
17. *Pastaza*, Yosa (coordinates not available), USNM 548227*.

PERU (total 142)

18. *Cuzco*, Armihuari, Camisea, La Convención (11°51′S, 72°46′W), MUSM 14070–14072; USNM 577953.
19. *Cuzco*, Konkariari, Camisea, La Convención (11°48′S, 72°52′W), MUSM 14851–14852.
20. *Cuzco*, Pagoreni, Camisea, La Convención (11°42′S, 72°54′W), MUSM 14073; USNM **582872***.
21. *Cuzco*, San Martín, Camisea, La Convención (11°47′S, 72°42′W), MUSM 14074–14078; USNM 577954.
22. *Cuzco*, Pichari, La Convención (12°30′S, 73°48′W), MUSM 21422.
23. *Cuzco*, 15.9 km SW Pilcopata, Consuelo, Paucartambo (13°08′S, 71°15′W), FMNH 123915–123916, **174914**; MUSM 19802.

24. *Cuzco*, Collpa de San Lorenzo, Quispicanchi (13°24′S, 70°46′W), FMNH 93579.
25. *Cuzco*, Huajyumbe, Quispicanchi (13°15′S, 70°35′W), FMNH 84414.
26. *Huánuco*, 9 km N Aucayacu, Huánuco (8°57′S, 76°07′W), TTU **46306**.
27. *Junín*, 2 mi NE of San Ramon, Chanchamayo (11°18′S, 75°20′W), AMNH 230649–230654*.
28. *Junín*, 3.2 km N of Rio Tulumayo, Vitoc, Chanchamayo (11°12′S, 75°20′W), USNM 507192*.
29. *Loreto*, Nearly oposite mouth of Huallaga, Rio Marañon, San Lorenzo, Alto Amazonas (4°50′S, 76°40′W), BMNH 24.3.1.63* [Holotype of *Vampyrodes ornatus* Thomas, 1924].
30. *Loreto*, 2 km NW of mouth of Río Pastaza, Trueno, Alto Amazonas (2°53′S, 72°24′W), MUSM 16407.
31. *Loreto*, Base Atun, Rio Samiria, Loreto (3°18′S, 74°37′W), FMNH 122905–122916; and Pithecia Biological Station, Rio Samiria, Loreto (=Base Atun, Rio Samiria, Loreto; same coordinates), FMNH 122903–122904.
32. *Loreto*, 1 km above Rio Tigrillo, Rio Tigre, Loreto (4°16′S, 74°19′W), FMNH 122917–122918.
33. *Loreto*, Campamento Catalino, Río Lagartococha, Maynas (coordinates not available), MUSM 21331
34. *Loreto*, Santa Luisa, Rio Nanay, Maynas (3°20′S, 74°35′ W), FMNH 87044.
35. *Loreto*, Quebrada Grande, Sucusari, Maynas (3°15′S, 72°55′W), MUSM 21329–21330.
36. *Loreto*, Río Samiria (coordinates not available), MUSM 3174.
37. *Loreto*, Tacshacocha, Río Samiria (coordinates not available), MUSM 1016–1017.
38. *Madre de Dios*, Hacienda Amazonia, Alto Rio Madre de Dios, Manu (12°56′S, 71°15′W), FMNH 125900–125915, 139566–139570, 139760, 139776*, 139777; MUSM 10100–10101, 10103–10108.
39. *Madre de Dios*, Above Rio Palotoa, Cerro de Pantiacolla, Manu (12°30′S, 71°22′W), FMNH 139785; MUSM 10102.
40. *Madre de Dios*, Maskoitania, 13.4 km NNW Atalaya, left bank Rio Alto Madre de Dios, Manu (12°46′S, 71°23′W), FMNH **174912–174913**, **174915***; MUSM 19801.
41. *Madre de Dios*, Estacion Biologica Pakitza, Parque Nacional del Manu, Manu (11°56′S, 71°17′W), MUSM 738–739, 5687, 12624–12625; USNM 566545*, 567158.
42. *Madre de Dios*, Quebrada Aguas Calientes, left bank Rio Alto Madre de Dios, 2.75 km E Shintuya, Manu (12°41′S, 71°15′W), FMNH 170250–170268; MUSM 16762–16771; MVZ **166596**, **192683**.
43. *Madre de Dios*, Desembocadura Río Blanco en el Río Tambopata Tambopata (coordinates not available), MUSM 20085.
44. *Pasco*, Palmira, Pozuzo, Oxapampa (10°03′S, 75°30′W), MUSM 10997–10998.
45. *Pasco*, Río Negro, Pozuzo, Oxapampa (coordinates not available), MUSM 10996.
46. *Pasco*, San Pablo, Oxapampa (coordinates not available), AMNH 230655*.
47. *Puno*, Santuario Nacional Pampas del Heath, Coasa, Carabaya (14°00′S, 69°58′W), MUSM 12867.
48. *Puno*, SE Río Tavara, Fila Boca Guacamayo, Carabaya (13°30′S, 69°41′W), USNM 579658.

49. *Ucayali*, Fundo Llanero, Sepahua, Atalaya (coordinates not available), MUSM 12809.
50. *Ucayali*, Fundo Texas, Sepahua, Atalaya (11°11′S, 72°59′W), MUSM 12810.
51. *Ucayali*, 59 km SW Pucallpa, Coronel Portillo (8°46′S, 74°9′W), USNM 499100*.
52. *Ucayali*, Río Ucayali, Pucallpa, Coronel Portillo (8°23′S, 74°32′W), MUSM 152.
53. *Ucayali*, 65 km NE of Pucallpa, West bank of río Shesha, Coronel Portillo (7°53′S, 74°49′W), MUSM 3168.

SURINAME (total 1)

54. *Sipaliwini*, Nassau camp (4°49′N, 54°36′W), TTU 106058.

TRINIDAD AND TOBAGO (total 6)

55. *Tobago*, Botanic Garden, Government Rest Home, Scarborough, Saint Andrew (11°11′N, 60°44′W), AMNH 175642*.
56. *Trinidad*, Las Cuevas, Saint George (coordinates not available), AMNH 256324*.
57. *Trinidad*, Mount Aripo, Saint George (10°43′N, 61°15′W), FMNH 51132*.
58. *Trinidad*, 4 mi N Arima, Simla Research Center, Saint George (10°41′N, 61°17′W), CM **94707**; TTU **44102**.
–. *Trinidad*, no specific locality, BMNH 89.6.10.2* [Holotype of *Vampyrops Caracciolæ* Thomas, 1901].

VENEZUELA (total 18)

59. *Amazonas*, Caño Essa, 56 Km NNW Esmeralda, Belen (3°37′N, 65°53′W), USNM 405117–405126*, 405128–405130*.
60. *Amazonas*, Río Orinoco, Tamatama (3°10′N, 65°49′W), USNM 408569, 545344.
61. *Bolivar*, Km 74, 59 Km SE El Dorado, El Manaco (6°17′N, 61°19′W), USNM 387186*.
62. *Bolivar*, 85 Km SSE El Dorado, km. 125 (5°59′N, 61°26′W), USNM 387185*.
63. *Miranda*, Birongo (10°29′N, 66°16′W), USNM 496565.

Vampyrodes major (total 363)

BELIZE (total 5)

64. *Toledo District*, Big Falls, N of Rio Grande River (16°15′N, 88°53′W), FMNH 120971.
65. *Toledo District*, Forestry Camp, Columbia Forest Preserve (16°16′N, 89°01′W), FMNH 58263*; USNM 506502; Columbia Forest Reserve, 2.1 km NNE of Salamanca, Columbia [= Forestry Camp, Columbia Forest Preserve; same coordinates], AMNH 256828*.
66. *Toledo District*, San Antonio (16°14′N, 89°01′W), FMNH 120970*.

COLOMBIA (total 97)

67. *Antioquia*, 25 Km S and 22 Km W of Zaragoza, La Tirana (07°18′N, 75°05′W), IAvH-M 927, 969, 971; USNM 499458–499461*.
68. *Cauca*, Betania, Alto Micay (2°40′N, 77°12′W), FMNH 113381, 113391.
69. *Cauca*, Quebrada Huanqui, Río Saija (2°52′N, 77°41′W), FMNH 104842.
70. *Chocó*, 4km abajo de la Italia (4°58′N, 76°13′W), UV 4583.
71. *Chocó*, Ensenada de Utria, Bahía Solano (4°04′N, 75°12′W), UV 3654–3655.

72. *Chocó*, Docordó, Itsmina (5°07′N, 76°50′W), ICN 11274.
73. *Chocó*, Parque Nacional de los Katios, Santata, Riosucio (7°26′N, 77°07′W), IAvH-M 3305, 4345–4347, 4859–4862.
74. *Valle del Cauca*, Río Zabaletas, across from village of Zabaletas, 29 Km SE Buenaventura (03°44′N, 76°57′W), ICN 6213; USNM 446857*, 446983–447014, 447017, 483657–483663*, 483664–483666, 483667–483684*, 484990*; UV 148, 351, 508, 581, 1186, 2286.
75. *Valle del Cauca*, El Hormiguero, 20 Km SE of Cali (3°19′N, 76°29′W), USNM 447016.
76. *Valle del Cauca*, El Mirador Subiendo Agua Sucia (Río Cajambre) margen derecha, Frente a Cerro Caja (3°32′N, 77°18′W), UV 3711.
77. *Valle del Cauca*, 10 mi NW Vijes, El Tambor (3°46′N, 76° 31′W), USNM 483685*.
78. *Valle del Cauca*, 2 km S Pance (3°19′N, 76°38′W), USNM 447015.
79. *Valle del Cauca*, Caimancito, Río Cajambre (coordinates not available), UV 3710.
80. *Valle del Cauca*, Río Raposo (3°43′N, 77°08′W), USNM 339401.

COSTA RICA (total 1)

81. *Puntarenas*, Llorona, Osa Peninsula (8°34′N, 83°30′W), USNM 526242*.

GUATEMALA (total 5)

82. *Izabal*, Escobas (15°41′N, 88°38′W), FMNH 41963–41964*, 41965–41966.
83. *Petén*, 25.6 km E Poptun, Finca La Union, Poptun (16°20′N, 89°25′W), USNM 564897*.

MEXICO (total 5)

84. *Oaxaca*, Sarabia River, 18 mi N of Matias Romero, Juchitan (17°08′N, 95°02′W), AMNH 186381*.
85. *Veracruz*, Tuxtla Mountains (18°33′N, 95°12′W), FMNH 127114*.
86. *Veracruz*, 1.7 km W Cerro Balzapote, Tuxtla Mountains (18°37′N, 95°04′W), FMNH 127112*, 127113.
87. *Veracruz*, Mirador (coordinates not available), USNM 6327.

NICARAGUA (total 3)

88. *Matagalpa*, Bijague (12°57′N, 85°26′W), AMNH 29431*.
89. *Zelaya*, 3 km NW Rama (11°30′N, 83°47′W), TTU **30642–30643**.

PANAMA (total 247)

90. *Bocas del Toro*, Almirante (9°18′N, 82°24′W), USNM 315546–315548*, 315549, 315550–315554*.
91. *Bocas del Toro*, Río Changena Camp (9°20′N, 82°15′W), USNM 319404, 319405–319412*, 319496*, 519716–519721.
92. *Bocas del Toro*, Sibube (9°36′N, 82°47′W), USNM 335254–335255*, 335256, 335257*, 519291–519297.
93. *Chiriquí*, 1 mi E Cuesta de Piedra (8°41′N, 82°38′W), USNM 331677–331681*, 331682.
94. *Colón*, 4.5 Km NW Frijoles, Bohio Peninsula (9°09′N, 79°50′W), USNM 503624–503627*.
95. *Colón*, 6 mi N Gamboa (9°07′N, 79°42′W), USNM 520554–520556*.

96. *Colón*, Isthmus of Panama, San Pablo (9°07′N, 79°47′W), MCZ 6756* [Holotype of *Vampyrodes major* Allen, 1908].
97. *Darién*, Rancho Frio, Darien National Park (7°52′N, 77°47′W), FMNH 128137–128140.
98. *Darién*, Junction rios Jaque and Imamado, Jaque (7°31′N, 78°11′W), USNM 362910*, 362911, 362912–362917*.
99. *Darién*, Mono Station, Darien National Park (7°44′N, 77°32′W), USNM 565913*.
100. *Darién*, Near Jaque, Pina Point (7°33′N, 78°12′W), USNM 314716, 314717*.
101. *Darién*, Río Chucunaque (8°09′N, 77°44′W), USNM 306731*.
102. *Darién*, Río Seteganti (7°28′N, 77°38′W), USNM 318127*.
103. *Darién*, Tacarcuna Village Camp (8°05′N, 77°17′W), USNM 309756–309760*, 309761, 309762–309768*, 309769, 309770–309786*, 309787, 309788–309803*, 309804, 309805*, 309806, 309807–309817*, 309818, 309819–309821*, 309822, 309823–309825*, 309826–309827, 309828–309832*, 309833, 309834–309835*, 309836–309837, 309838–309842*, 309843, 309844–309855*, 309856, 309857–309859*, 309860–309862.
104. *Panamá*, Barro Colorado Island (9°09′N, 79°50′W), AMNH 239254; USNM 304896*, 304897–304901*, 332051*, 457951*, 503836*, 514964–514965*, 514980*, 539811–539812*, 544890*.
105. *Panamá*, Cerro Azul (9°13′N, 79°18′W), USNM 306729–306730*, 323442–323444*.
106. *San Blas*, Quebrada Venado, Armila (8°40′N, 77°32′W), USNM 335258–335262*, 335263, 335264–335274*, 519298–519331.

Chiroderma villosum (total 1)

PERU

107. *Madre de Dios*, Maskoitania, 13.4 km NNW Atalaya, left bank Rio Alto Madre de Dios, Manu (12°46′S, 71°23′W), FMNH **174652**.

Platyrrhinus lineatus (total 1)

PARAGUAY

108. *Paraguarí*, Sapucaí (25°40′S, 56°55′W), AMNH 23771.

Platyrrhinus recifinus (total 1)

BRAZIL

109. São Paulo, Parque Estadual Ilhabelha, Ilha de São Sebastião (23°50′S, 45°18′W), MVZ **185607**.

Vampyressa melissa (total 1)

PERU

110. *Cuzco*, 15.9 km SW Pilcopata, Consuelo, Paucartambo (13°08′S, 71°15′W), FMNH **174910**.

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