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Filogenia e Revisão Sistemática de *Cynomops* (Chiroptera: Molossidae)

Phylogeny and Revisionary Systematics of *Cynomops* (Chiroptera: Molossidae)

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“In the search for scientific discoveries, every problem is an opportunity. The more difficult the problem, the greater the likely importance of its solution.”

Edward O. Wilson

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Índice

INTRODUÇÃO GERAL

Os morcegos de cauda-livre pertencentes à família Molossidae são insetívoros aéreos com distribuição pantropical, podendo ocorrer em regiões temperadas como o sul da Europa e Ásia, centro-sul dos Estados Unidos, Patagônia Argentina e Chile (Freeman 1981; Eger 2008). Atualmente, Molossidae é composta por 18 gêneros e mais de 100 espécies (Simmons 2005; Gregorin and Cirranello 2015), sendo a quarta família de Chiroptera mais rica em espécies. Ainda assim, a diversidade de Molossidae é subestimada, o que vem sendo comprovado dado às várias recentes descrições de novas espécies (e.g., *Mormopterus eleryi* [Reardon *et al*. 2008]; *Eumops wilsoni* [Baker *et al*. 2009]; *Molossus alvarezi* [Gonzalez-Ruiz *et al*. 2011]; *Eumops chiribaya* [Medina *et al*. 2014]) e redescrições de táxons antes descritos como subespécies (e.g. *C. mexicanus*, *Promops davisoni*, *Molossus barnesi*).

Os morcegos pertencentes ao gênero *Cynomops* forrageiam em espaços abertos, livre de obstáculos, onde o voo em alta velocidade aliado aos chamados de ecolocação em alta frequência permitem o sucesso na captura das presas (Freeman, 1981; Bogdanowicz *et al*., 1999). Ainda, as espécies que compõem o gênero são classificadas como sinantrópicas por serem comumente encontradas em ambientes antropizados (eg. casas abandonadas, mourões de cerca, frestas em telhados e postes) (Vizotto and Taddei, 1976; Bader *et al*., 2015). *Cynomops*, até a presente revisão, era composto por cinco espécies (*sensu* Simmons 2005), *Cynomops abrasus* (Temminck, 1827), *Cynomops greenhalli* Goodwin, 1958, *Cynomops mexicanus* (Jones and Genoways, 1967), *Cynomops paranus* (Thomas, 1901), e *Cynomops planirostris* (Peters, 1865) que ocorrem em grandes extensões pela região

Neotropical, desde o sul do México até o Paraguai e Norte da Argentina, incluindo Trinidad e Tobago (Fig. 1, IUCN 2012). Uma sexta espécie, *C. milleri* (Osgood, 1914), tinha status taxonômico em debate, sendo tratada ora como subespécie de *C. planirostris* (Koopman, 1978), ora sinonimizada com *C. paranus* (Simmons and Voss, 1998), ou, finalmente, considerada como espécie (Eger, 2008).

Figura 1. Distribuição geográfica das espécies do gênero *Cynomops* conforme dados da IUCN 2014.

Ainda dentre as espécies, *C. abrasus* aparentava ser um complexo de espécies considerando a distribuição geográfica e as dimensões corporais e cranianas de seus holótipos e era composta, anteriormente a este trabalho, por quatro subespécies: *C. a. mastivus*, do Escudo das Guianas, *C. a. brachymeles*, do leste do Peru e Bolívia, *C. a. cerastes*, do Paraguai e norte da Argentina e *C. a. abrasus* do leste do Brasil.

O presente trabalho reúne as revisões de *Cynomops*, tratando o problema de *C. milleri*, testando o complexo de espécies de *C. abrasus*, e apresentando hipóteses de relações filogenéticas para *Cynomops* por meio da análise de um número expressivo de espécimes abrangendo toda a distribuição geográfica conhecida para as espécies e subespécies de *Cynomops*.

O trabalho está dividido em dois artigos; o primeiro aborda a sistemática filogenética, elucidando as relações evolutivas de *Cynomops* e testando o monofiletismo de *Cynomops abrasus* baseado em análise combinada de dados moleculares e morfológicos. O segundo artigo tem como foco a revisão taxonômica, visando identificar quantas e quais espécies compõem o complexo de espécies de pequeno porte de *Cynomops*.

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Phylogeny of dog-faced bats (Molossidae: *Cynomops*) with revalidation of *C. mastivus* Thomas

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Abstract

The low representativeness of the dog-faced bats (genus *Cynomops*) in collections has constrained the taxonomic comprehension of some taxa, in particular the large sized *Cynomops abrasus*. This species currently encompasses four subspecies widespread distributed in South America: *C. a. abrasus*, *C. a. brachymeles*, *C. a. cerastes* and *C. a. mastivus*. Here, we evaluated the status of these four subspecies and also the phylogenetic relationships within the genus *Cynomops* using complete sequences of two mitochondrial genes (Cyt *b* and COI) and 39 morphological characters. Maximum parsimony, maximum likelihood and Bayesian analyses of these data recovered a novel phylogenetic hypothesis for *Cynomops*, supported the recognition of *C. a. mastivus* as a distinct species, separated from *C. abrasus*, and uncovered two previously unknown lineages of *Cynomops*. The use of mitochondrial genes combined with morphological characters was a powerful tool to recover the phylogenetic relationships within *Cynomops* and demonstrated that the genus is much more diverse than previously though.

Keywords: free-tailed bats; Neotropical; systematics; *Cynomops abrasus*; mtDNA; morphology.

1. Introduction

The Neotropical dog-faced bats from the genus *Cynomops* Thomas, 1920 (Chiroptera: Molossidae) are fast flying, aerial insectivores that hunt in open spaces, usually above the canopy level in forested habitats (Kalko *et al*., 1996), and form small colonies of up to 14 individuals (Vizotto and Taddei, 1976; Esbérard and Bergallo, 2005). Due to their foraging behavior, and low local abundance, *Cynomops* is rarely captured in ground level mist-nets and consequently little represented in collections (Peters *et al*., 2002).

As recognized by Simmons (2005) and Eger (2008) the genus is composed by six species including *Cynomops abrasus* (Temminck, 1827), *Cynomops greenhalli* Goodwin, 1958, *Cynomops mexicanus* (Jones and Genoways, 1967), *Cynomops milleri* (Osgood, 1914), *Cynomops paranus* (Thomas, 1901), and *Cynomops planirostris* (Peters, 1865). The geographical range of *Cynomops* extends from southern Mexico to Paraguay and northern Argentina, including Trinidad and Tobago (Goodwin and Greenhall, 1961; Koopman, 1982; Alvarez-Castañeda and Alvarez, 1991; Eger, 2008).

The taxonomic history of *Cynomops* is complex, and the genus itself has previously been considered a subgenus of *Molossops* (Cabrera 1958; Goodwin and Greenhall, 1961; Freeman, 1981; Koopman, 1993, 1994; Simmons and Voss, 1998). *Cynomops* contained three species up to the 1990's (Koopman, 1993), *C. planirostris*, *C. abrasus* and *C. greenhalli*, but variations within their populations has led to the descriptions of a series of subspecies (Simmons, 2005). More recently, based on parsimony analysis of restriction enzyme data, Peters *et al*. (2002) recognized *Cynomops* as a separate genus from *Molossops*, and provided evidences to the recognition of *C. paranus* (previously suggested

by Simmons and Voss, 1998) and *C. mexicanus* as full species, from respectively, *C. planirostris* and *C. greenhalli*.

The status of some forms of *Cynomops* has also been subject of debate. Simmons and Voss (1998) recognized *C. paranus* as a distinct species from *C. planirostris* and Eger (2008) provided evidences to the recognition of *C. milleri*, a taxon in dispute by some other authors (see Koopman, 1978, 1993, 1994; Simmons and Voss, 1998). Historically, no other *Cynomops* have been more controversial than *Cynomops abrasus* (Sanborn, 1932; Cabrera, 1958; Husson, 1962; Carter and Dolan, 1978; Simmons, 2005; Eger, 2008).

The diversity included within *C. abrasus* is currently described by four subspecies distributed throughout South America: *Cynomops abrasus mastivus* (Thomas, 1911) from the Guiana Shield, *Cynomops abrasus brachymeles* (Peters, 1865) from eastern Peru and Bolivia, *Cynomops abrasus cerastes* (Thomas, 1901) from southern Brazil, Paraguay and northern Argentina, and the nominal form restricted to eastern Brazil (Cabrera, 1958; Simmons, 2005; Eger, 2008). The subspecies of *C. abrasus* were separated based primarily on body size (Cabrera, 1958; Koopman, 1994).

Although the monophyly of *Cynomops* has been recovered in recent studies (Peters *et al*., 2002; Ammerman *et al*., 2012; Gregorin and Cirranello, 2015), a single study of the interrelationships within the genus is available (Peters *et al*. 2002) with minor representativeness of *C. abrasus*, not including samples of *C. a. abrasus*, *C. a. brachymeles,* and *C. a. cerastes* subspecies.

Herein, we tested the monophyly of *Cynomops abrasus* as currently known using complete sequences of Cytochrome *b*, Cytochrome oxidase subunit I, and morphological characters, proposing a new framework for the understanding of the evolutionary relationships within the genus *Cynomops*.

2. Materials and methods

2.1. Taxon sampling

We analyzed specimens and obtained DNA sequence data from individuals representative of all currently recognized *Cynomops* species, and all subspecies described for *C. abrasus*. Outgroup taxa included *Eumops auripendulus*, *Molossops temminckii* and *Mormopterus kalinowskii*. A complete list of the specimens studied is provided in the Supplementary Information (Appendixes A and B).

The material studied is deposited in the following collections: American Museum of Natural History, New York, USA (AMNH); Biodiversity Institute, University of Kansas, Lawrence, USA (KU); Instituto Nacional de Pesquisas na Amazônia, Manaus, Brazil (INPA); Field Museum of Natural History, Chicago, USA (FMNH); Mammal collection of Universidade Federal de Lavras, Lavras, Brazil (CMUFLA); Mammal collection of Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (CMUFMG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Natural History Museum, London, UK (BMNH); Royal Ontario Museum, Toronto, Canada (ROM); Museum of Texas Tech University, Lubbock, Texas, USA (TTU/TK); Universidade Federal Rural do Rio de Janeiro, Seropédica, Brazil (ALP); Laboratório de Diversidade de Morcegos da Universidade Federal Rural do Rio de Janeiro, Seropédica, Brazil (LDM), Universidade Estadual Paulista, São José do Rio Preto, Brazil (DZSJRP); and United States National Museum of Natural History, Washington DC, USA (USNM). Tissue samples are housed in the frozen tissue collection of the ALP; AMNH; Au Institut des Sciences de l'Évolution, Montpellier, France (ISEM); CMUFLA; CMUFMG; Colección Regional Durango, Instituto Politécnico Nacional, Durango, Mexico (CRD); FMNH; Museo de Historia Natural de la Universidad Nacional San Agustín, Arequipa, Peru (MUSA); Museo

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2.2. Morphological data

We used 39 discrete morphological characters, including 30 modified from Velazco (2005), Giannini and Simmons (2007a), Tavares (2008), Tavares *et al*. (2014), Gregorin (2009), and Gregorin and Cirranello (2015). A matrix containing all morphological characters used is presented in Table 1, and a characters description list is provided in the Appendix C. Anatomical terminology follows Freeman (1981) and Giannini *et al*. (2006). For tooth nomenclature, we follow Giannini and Simmons (2007b) assuming that the second lower premolar is lost in Chiroptera, and Gregorin and Cirranello (2015) considering the premolar arrangement of p1, p4 and p5 for molossids.

The glans used to score the penis characters were prepared for scanning electron microscopy by removing the prepuce (outer sheath and inner prepuce) (Ryan 1991a), rinsing overnight in water followed by dehydration through a graded series of alcohol to 100% (50, 70, 80, 90, and 100). The material was kept by 15 minutes in each bath, except by the last step (alcohol 100%) that was made twice. Specimens then were dried to the critical point in CO_2, mounted on a metal stub, coated with gold, and photographed in a LEICA Stereoscan 440 (Scanning Electron Microscopy Laboratory, Smithsonian Institution - Washington, DC) and JEOL JSM-6360L (Microscope Center of Universidade Federal de Minas Gerais - Brazil). The nomenclature of the glans penis and its structures follows Ryan (1991a, b).

Table 1. Morphological matrix. Question marks "?" are missing data, dashes "–" are characters not applicable to a particular taxon and forward slash "/" are polymorphic state.

Taxon/ character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Eumops	1	1	0	1	1	1	0	1	1	2	0	1	0	1	1	0	0	1	0	1	-	0	-
Mormopterus	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	-
Molossops	0	1	2	0	0	0	2	1	0	1	1	1	1	1	1	0	1	1	1	1	0	1	1
C. abrasus†	1	1	1	0	0	1	0	1	0	2	0	1	1	1	1	1	1	1	1	1	1	1	1
C. a. mastivus	1	1	1	0	0	1	0	1	0	2	0	1	1	0	1	1	1	1	1	0	2	1	0
C. greenhalli	1	1	1	0	0	0	1	1	0	2	0	1	1	0	1	1	1	1	1	0	2	1	1
C. mexicanus	1	1	1	0	0	0	2	1	0	2	0	0	0	0	1	1	1	1	0	1	1	1	0
C. milleri	1	1	1	0	0	0	1	1	0	2	0	1	1	0	1	1	1	1	1	1	2	1	1
C. paranus	1	1	1	0	0	0	1	1	0	2	0	1	1	0	1	1	1	1	0/ 1	1	1/ 2	1	0/ 1
C. planirostris	1	1	1	0	0	0	3	1	0	2	0	0/ 1	1	0	1	1	1	1	1	1	1	1	0

† We did not detected variations worthy of separations among populations of *C. abrasus* within Brazil (include subspecies *C. a. abrasus* and *C. a. brachymeles*) and from Paraguay (*C. a. cerastes*) and lumped those subspecies in the matrix as *C. abrasus*.

Table 1. (Continued)

Taxon/ character	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Eumops	0	0	0	1	2	1	0	1	?	?	0	-	0	-	0	0
Mormopterus	0	0	0	1	0	1	0	0	?	?	0	-	0	-	1	0
Molossops	0	1	1	1	1	0	0	1	1	0	1	1	0	0	1	0
C. abrasus†	0	1	1	0	-	0	0	2	0	2	1	0	1	1	1	1
C. a. mastivus	0	1	1	0	-	0	1	2	0	2	1	0	1	1	1	1
C. greenhalli	1	1	1	0	-	0	1	2	0	2	1	0	1	1	1	1
C. mexicanus	2	1	1	1	0	0	1	2	?	?	?	?	?	?	?	?
C. milleri	1	1	1	0	-	0	1	2	0	2	?	?	?	?	?	?
C. paranus	1	1	1	0	-	0	1	2	0	2	1	0	0	1	1	1
C. planirostris	0	1	1	1	0	0	1	2	0	1	1	1	0	0	0	1

We recorded external and craniodental measurements in millimeters (mm) using digital calipers accurate to 0.01 mm; body mass is in grams (g). Standard external measurements (TL, total length; HF, hind foot length; E, ear length; and body mass) were taken from skin labels or database records. Measurements are defined as follows:

Forearm length (FA), distance from the tip of the olecranon process to wrist (including carpals), and taken with the wing partially folded.

Greatest length of the skull (GLS), distance from the posteriormost point at the occipital bone to the most anterior point on the rostral-most bone.

Braincase breadth (BB), greatest breadth of braincase.

Mastoid breadth (MB), greatest breadth across mastoid region.

Rostral width (ROS), greatest breadth across the lacrimal ridges.

Condyloincisive length (CIL), distance from the posteriormost margins of occipital condyles to the anterior face of upper incisor(s).

Zygomatic breadth (ZB), greatest breadth across zygomatic arches

Postorbital breath (POB), least breadth measured in the postorbital region, always posterior to the postorbital process when present.

Maxillary toothrow length (MTRL), distance from the anterior face of the upper canine to the most posterior edge of the last upper molar.

Breadth across upper molars (BM), least breadth across the last upper molars.

Width across upper canines (C-C), least width across the upper canines.

Mandible length (ML), from the mandibular symphysis to the condyloid process.

2.3. DNA extraction

Genomic DNA was isolated from liver, muscle, brain or patagium tissue samples, and DNA extractions were performed with a standard phenol–chloroform–isoamyl alcohol protocol (Sambrook *et al*., 2001) or with DNeasy® extraction kits (Qiagen®). For *C. milleri* (USNM 387744) and *Cynomops* sp. 1 (USNM 319084), the DNA was extracted from dried skins according to the methods described in Wisely *et al*. (2004) and all pre-PCR protocols were conducted in the genetic laboratory for ancient DNA at the Center for Conservation and Evolutionary Genetics at the Smithsonian Institution, Washington, DC.

2.4. DNA sequencing

Cytochrome *b* (Cyt *b* - 1140 bp): For preserved tissue samples PCR amplifications were carried out in 15 µL reactions containing 40–60 ng of DNA, 0.3U of Platinum Taq (Invitrogen®), 1x Platinum Taq PCR buffer, 1.5 µM $MgCl_2$, 200 µM dNTPs set (Invitrogen®) and 0.3 µM of each primer. The primers used for amplifications were L14121 and H15318, and two additional internal primers – MVZ4 and L14881 – were used for sequencing reactions (Table 2). We used the following cycling scheme for PCR: 5 min at 94°C followed by 35 cycles of 30 s at 94°C, 40 s at 50°C for primer annealing and 85 s at 72°C for extension, and a final 10 min extension at 72°C after the last cycle. To amplify DNA from dried skin samples, PCR amplifications were carried out in 25 µL reactions containing 0.3 µL TaqGold (5 units µL-1, Applied Biossystems, Foster City, CA, USA), 1 µL per primer (10 µL), 0.5 µL dNTP (10 µM), 2 µL MgCL2 (25 mM), 2.5 µL Ampli Taq Buffer (Applied Biossistems), 4 µL BSA (0.01 mg/ µL), 3 µL gDNA, and 10.7 µL sterile water. For PCR and sequencing reactions we used internal primers designed for this study based on the sequences generated from the preserved tissues samples (Table 2). We used

the following cycling scheme for PCR: 10 min at 95°C followed by 55 cycles of 1 min s at 94°C, 1 min at 50 °C for primer annealing and 1 min at 72°C for extension, and a final 10 min extension at 72°C after the last cycle.

Table 2. Primers used in this study for amplification and/ or sequencing.

Gene	Primers	Sequence (5' – 3')	Length (bp)	Reference
Cyt *b*	L14121	GACTAATGACATGAAAAATCA	1140	Redondo *et al*. (2008)
	H15318	TATTCCCTTTGCCGGTTTACAAGACC		
Cyt *b*	MVZ4	GCAGCCCCTCAGAATGATATTTGTCCTC	610	Smith and Patton, 1993
	L14881	GACATAATTCCATTCCACCCCTAC		Redondo *et al*. (2008)
Cyt *b*	CYNH1	GTATCRGATGTRTARTGTATTGCTAGG	176[1]	This study
Cyt *b*	CYNL2	GAAAYTTCGGCTCYCTYTTAGG	223	This study
	CYNH2	CCATARTAGAGYCCGCGTCC		
Cyt *b*	CYNL3	CCAAYGGRGCYTCAATATTC	262	This study
	CYNH3	TCTACTGAGAAGCCYCCTCAG		
Cyt *b*	CYNL4	CTGCAATYCCCTAYATYGGAAC	301	This study
	CYNH4	CCTAGRAGGTCRGGRGARAAT		
Cyt *b*	CYNL5	CTGAYATAATCCCYTTYCAYCC	226	This study
	CYNH5	CCTCCTARTTTRTTRGGGATTG		
Cyt *b*	CYNL6	CCTYCTAGGAGACCCYGACAA	235	This study
	CYNH6	TCARAATAGGCAYTGGCTTAG		
Cyt *b*	CYNL7	CACACYTCHAAACAACGAAG	224[2]	This study
COI	COX-L2	TGTCTTTAGATTTACAGTCTAATGC	1300	Lara-Ruiz *et al*. (2008)
	H8121	GGGCAGCCRTGRATTCAYTC		Sorenson, 2003
COI	LCO1490	GGTCAACAAATCATAAAGATATTGG	657	Folmer *et al*. 1994
	COXIH	ACTTCAGGGTGTCCGAAGAATCA		Lara-Ruiz *et al*. (2008)

[1] Combined with L14121; [2] Combined with H15318

Cytochrome oxidase (COI - 1357 bp): The reagents used and their concentrations were the same as above for preserved tissue samples. The primers used for amplifications were COX-L2 and H8121, and two additional internal primers – LCO1490 and COXIH – were

used for sequencing reactions (Table 2). We used the following cycling scheme for PCR: 5 min at 95°C followed by 35 cycles of 1 min at 95°C, 1 min at 50 °C for primer annealing and 1 min and 30 s at 72°C for extension, and a final 10 min extension at 72°C after the last cycle. We were unable to sequence the COI from the dried skin samples.

PCR products of tissue samples were sequenced using a 10 µL reaction mixture including 4 µL of PCR product, 2 µL of primer (2.5 µM), 1.5 µL Big Dye 5 x Buffer (Applied Biosystems), 1 µL Big Dye version 3 (Applied Biosystems). The reaction was run using a thermal cycler with denaturation at 96°C for 10 s, annealing at 50°C for 5 s and extension at 60°C for 4 min, repeated for 26 cycles.

The mixture for the dried skin PCR products contained 1 µL of PCR product, 0.5 µL primer (10 µM), 1.75 µL Big Dye 5 x Buffer (Applied Biosystems), 0.5 µL Big Dye version 3.1 (Applied Biosystems), and 6.25 µL sterile water. The reaction was run using a thermal cycler with denaturation at 95°C for 30 s, annealing at 50°C for 30 s and extension at 60°C for 4 min, repeated for 30 cycles.

Cycle-sequencing products of tissue samples were purified through an EtOH–EDTA precipitation protocol and the dried skin samples were cleaned using sephadex centrifugation protocol. The sequences of both strands were carried out in an ABI 3130 (Applied Biosystems®) automated sequencer using Big Dye Terminator Cycle Sequencing methodology (Applied Biosystems®). The sequences produced in this study will be deposited on GenBank.

2.5. Phylogenetic analyses

Sequences were assembled and checked for quality using DNA Baser Sequence Assembler v4 (2013), and aligned using the Muscle algorithm (Edgar, 2004) implemented

in MEGA 5.05 (Tamura *et al*., 2011). MEGA 5.05 was also used to calculate intraspecific and interspecific genetic distances for Cyt *b* with a Kimura 2-parameter (K2P) model (Kimura, 1980).

We conducted Maximum Parsimony (MP) analyses for the combined molecular and morphological data using the heuristic search algorithm implemented in an intel-based version of PAUP* 4.0B10 (Swofford, 2002). Each search was conducted with 1,000 iterations of the heuristic search algorithm with random taxon addition and TBR branch swapping. All characters were equally weighted in all analyses. As a measurement of support we calculated bootstrap values (Felsenstein, 1985) with 1,000 pseudoreplicates using a heuristic search with 100 random additions.

Partition Finder 1.0.1 (Lanfear *et al*., 2012) was used to select the best partitions and models of sequence evolution using the Akaike Information Criterion (AIC; Akaike, 1974). We defined separate data blocks for the three codon positions for both genes.

Maximum Likelihood (ML) analyses were performed using RAxML 7.2.8 through the Cipres portal (Miller *et al*., 2010; Stamatakis, 2006). The ML was implemented using the General Time Reversible model, with among site rate variations estimated by discrete gamma categories (GTR+I+G) (Stamatakis, 2006). Bootstrap resampling was used to assess support for the tree nodes.

We conducted Bayesian Inference analyses using MrBayes 3.1.2, and the best-fit partitioning schemes and models for each dataset as retrieved by the Partition Finder runs. To the morphological data partition in the combined Bayesian analyses, we used the standard stochastic model (Mkv) (Lewis, 2001). The number of generations needed to be run and the burn-in were determined by examining the log likelihood (lnL) plots as provided by the software Tracer 1.6 (Rambaut and Drummond, 2007). Four simultaneous

Markov chains (one cold and three heated) were run for 20 million generations, with trees sampled every 200 generations, and the first 10% of the generations discarded as "burn-in".

2.6. Hypothesis testing

We assessed significance of differences between the phylogenetic hypotheses available (ours and that of Peters *et al*., 2002) using the approximately unbiased test (AU) as implemented in the software *Consel* (Shimodaira, 2002). The input trees to be compared were calculated in RAxML using the *constraint* command.

3. Results

Best-fitting models of sequence evolution for each gene and partition are summarized in Table 3.

Table 3. Dataset characteristics and best-fitting models of nucleotide substitution.

Dataset	Terminals	Base pairs/ characters	Invariant sites	Parsimony informative sites	Selected models/ partition
Cyt *b*	77	1140	750	308	GTR + I + G for 1st position, GTR + I for 2nd, GTR + I + G for 3rd
COI	59	1357	965	336	GTR + I + G for 1st position, HKY for 2nd, GTR + G for 3rd
mtDNA	84	2497	1715	644	GTR + I + G for 1st_CYTB, GTR + I for 2nd _CYTB, GTR + I + G for 3rd_CYTB; GTR + I + G for 1st_COI, HKY for 2nd COI, GTR + G for 3rd_COI
Morphology	85	39	22	17	Mkv

Most nodes were recurrently supported in all analyses (Fig. 1; Supplementary information, Fig. 1) with virtually no incongruences. Combined data including the mtDNA datasets produced the same results as the combination of molecular and morphological

data, with the exception that morphological data provide more robust support values for the node containing the clades C (*C. paranus* and *Cynomops* sp. 1) and D (*C. abrasus*, *C. a. mastivus* and *C. greenhalli*) (Fig. 1; PP = 0.97; BP = 68) (Fig. 1; Supplementary information, Fig. 1).

The monophyly of *Cynomops* was fully supported by our combined data (Fig. 1) that also recovered full support for most of the internal clades (Fig. 1). A total of seven morphological characters support the clade of *Molossops* and *Cynomops*, and four synapomorphies support the monophyly of *Cynomops* (Table 1, Appendix C). The clade A (Fig. 1) consists of a basal *C. mexicanus* to a nested clade containing individuals from Colon and Pacora (Panama) previously identified as *C. paranus* and *C. greenhalli* identified provisionally as "*Cynomops* sp. 1" (Fig. 1). Clade B consists of *C. planirostris* from several localities (from Upper Takutu-Upper Essequibo, Guyana to Ñeembucu, Paraguay); clade C contains a paraphyletic arrangement of *C. paranus* and *C. milleri* from the Guiana Shield, as sister group to a series of *Cynomops* from the eastern Andes of Ecuador, identified as "*Cynomops* sp. 2" (Fig. 1); and clade D splits into two main clades, recovering paraphyly of *C. abrasus*.

Within clade D, one branch is composed by individuals representing *C. abrasus mastivus* and *C. greenhalli*, and the second contains *C. abrasus* from several localities (from Madre de Dios, Peru to Itapúa, Paraguay). *Cynomops abrasus mastivus* (from Guiana Shield, Ecuador and northwestern Brazil) is clearly separated from the large clade containing representatives from other subspecies of the *C. abrasus*, including *C. a. abrasus* (southeastern Brazil), *C. a. brachymeles* (southeastern Peru), and *C. a. cerastes* (Paraguay) (Fig. 1).

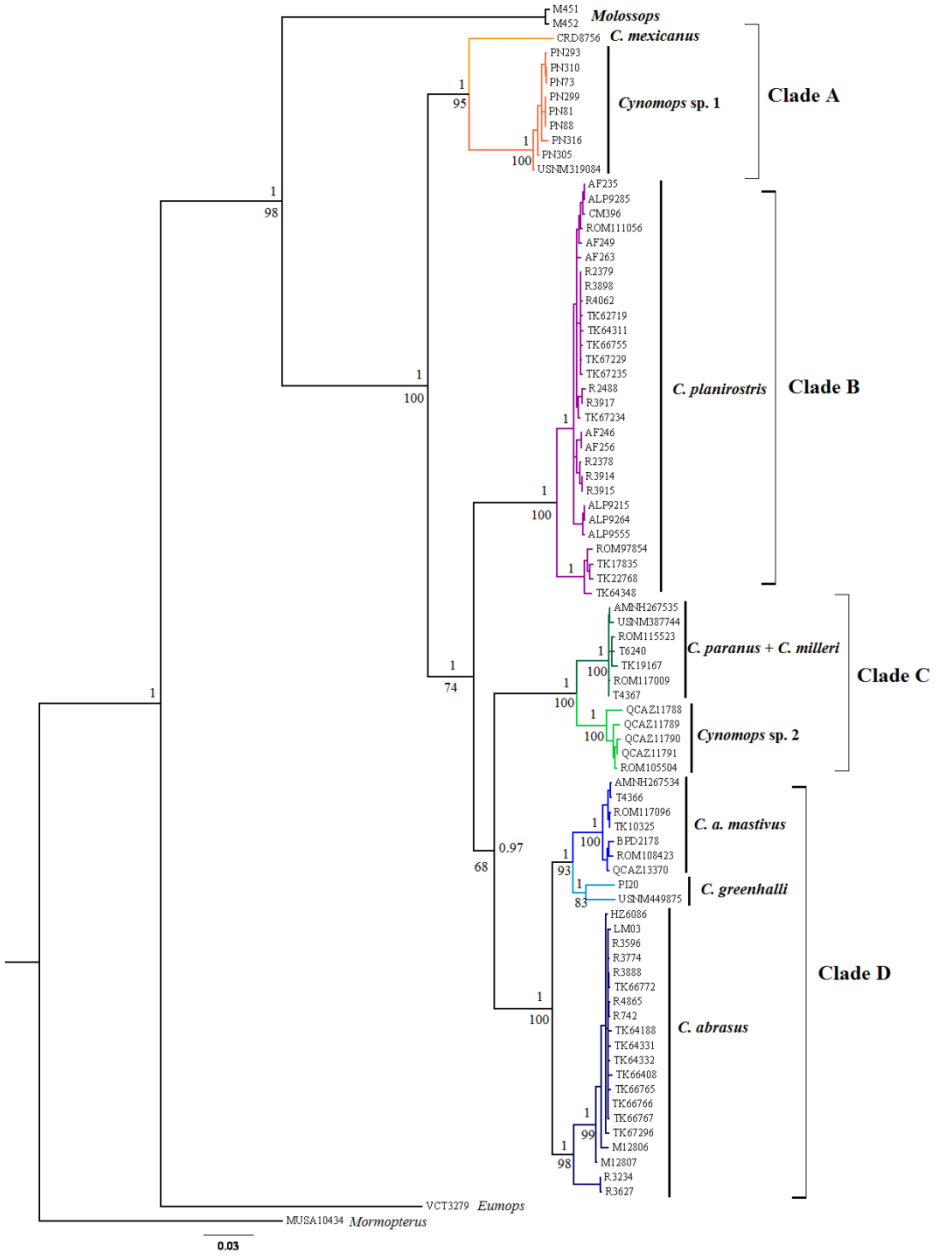

Figure 1. Bayesian tree of *Cynomops* species generated with 2497 base pairs of the mtDNA (COI + Cyt *b*) and 39 morphological characters. Values above branches represent Bayesian posterior probabilities (PP) and below branches, the maximum-parsimony (MP) bootstrap. See Appendix B for museum acronyms and collection sites.

The *Approximately Unbiased* (AU) tests comparing our tree topology and the hypothesis proposed by Peters *et al*. (2002) did not rule out Peters's (2002) topological arrangements (δLnl= 2.3; AU= 0.279).

Intraspecific genetic distances for the Cyt *b* gene varied from 0.4% to 3.7% (Table 4). Within *C. greenhalli* we found individual differences with *p*-distance of 3.7% between individuals from Panama, and from the western Andes of Ecuador. A mean *p*-distance of 3.0% was also found between two haplogroups of *C. planirostris* from Guiana Shield + Peru, and an individual from Ñeembucu, Paraguay –and Eastern Brazil + Paraguay (Fig. 1). Additionally, two individuals of *C. abrasus* from São Paulo (R3234 and R3627) formed a basal clade to the large *C. abrasus* clade (Fig. 1, clade D), and were 3.3% genetically divergent compared to the remaining individuals of *C. abrasus* (Fig.1 and appendix B). Values for interespecific variation ranged from 4.6% (*C. greenhalli vs C. a. mastivus* and *C. paranus vs Cynomops* sp. 2) to 12.5% (*Cynomops* sp.1 *vs Cynomops* sp.2), and the lowest genetic distance measured was observed between *C. paranus* and *C. milleri* (0.6%).

Table 4. Average Kimura 2-parameter distances (%) between species of *Cynomop*s based on 1140 base pairs of the Cyt *b*. Intraspecific divergence is on the diagonal.

	n	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1. *C. abrasus*	16	**1.1**								
2. *C. greenhalli*	2	5.8	**3.7**							
3. *C. mastivus*	7	4.9	4.6	**1.0**						
4. *C. mexicanus*	1	11.4	11.6	11.9	-					
5. *C. milleri*	1	9.0	9.9	9.7	11.9	-				
6. *C. paranus*	6	8.9	9.9	9.6	11.6	0.6	**0.4**			
7. *C. planirostris*	24	8.9	9.3	9.6	11.5	9.7	9.7	**1.6**		
8. *Cynomops* sp. 1	9	10.6	10.6	10.9	7.9	12.3	12.3	11.0	**0.6**	
9. *Cynomops* sp. 2	5	9.8	10.2	9.7	12.0	4.7	4.6	10.6	12.5	**1.1**

The paraphyly of *C. abrasus* (*lato sensu*) and a set of morphological characters that distinguish both lineages (*mastivus* and the remaining *abrasus*) indicate that *C. mastivus* is

a distinct species that merits recognition apart from *C. abrasus*, and we provide herein a redescription, and an emended diagnosis for this taxon.

Cynomops mastivus (Thomas, 1911)

Mastiff´s Dog-faced Bat

Figures 3–6

Molossops mastivus Thomas, 1911: 113, type locality "Bartica Grove, lower [Río] Essequibo", Cuyuni-Mazaruni, Guyana.

Cynomops mastivus: Thomas, 1920:189; first use of current name combination.

Molossops [(*Cynomops*)] *brachymeles mastivus*: Cabrera, 1958: 119; name combination.

Cynomops abrasus: Husson, 1962: 246; not Temminck, 1827.

Molossops [(*Cynomops*)] *abrasus mastivus*: Williams and Genoways 1980: 233; name combination.

Cynomops abrasus [*mastivus*]: Simmons, 2005; name combination

TYPE MATERIAL: The holotype BMNH 10.11.10.3 is a relatively well-preserved skin and a skull of an adult male from Bartica Grove, lower Essequibo, Cuyuni-Mazaruni, Guyana, collected by Mr. Crozier and brought to the British Museum in 1910 by F. V. McConnell (Lim and Catzeflis, 2014). The date of the capture and other information are not provided in the label.

MEASUREMENTS OF THE HOLOTYPE: FA 48.00, GLS 23.12, POB 5.73, ROS 10.81, C-C 6.85, ZB 16.20, BB 10.68, MB 15.58, MTRL 8.64, BM 10.24, CIL 22.95, ML 17.31. Additional measurements (mm) are from Thomas (1911): Third metacarpal length 49, fifth metacarpal 26, first phalanx of third metacarpal 11.5, interorbital breadth 5.5, height of the canine 4.8, and height of lower jaw below m1 3.5.

DISTRIBUTION: As defined here, *Cynomops mastivus* is known from the lowlands (5–534 m a.s.l.) of northern South America, on the eastern slopes of the Andes in Venezuela, Guyana, Surinam, French Guiana, Ecuador, and the Brazilian Amazonia (Fig. 2). The only specimen analyzed from Colombia, southwestern Andes, labelled as "*abrasus*" (FMNH 89574) is a young male with damaged skull and its identity could not be securely determined.

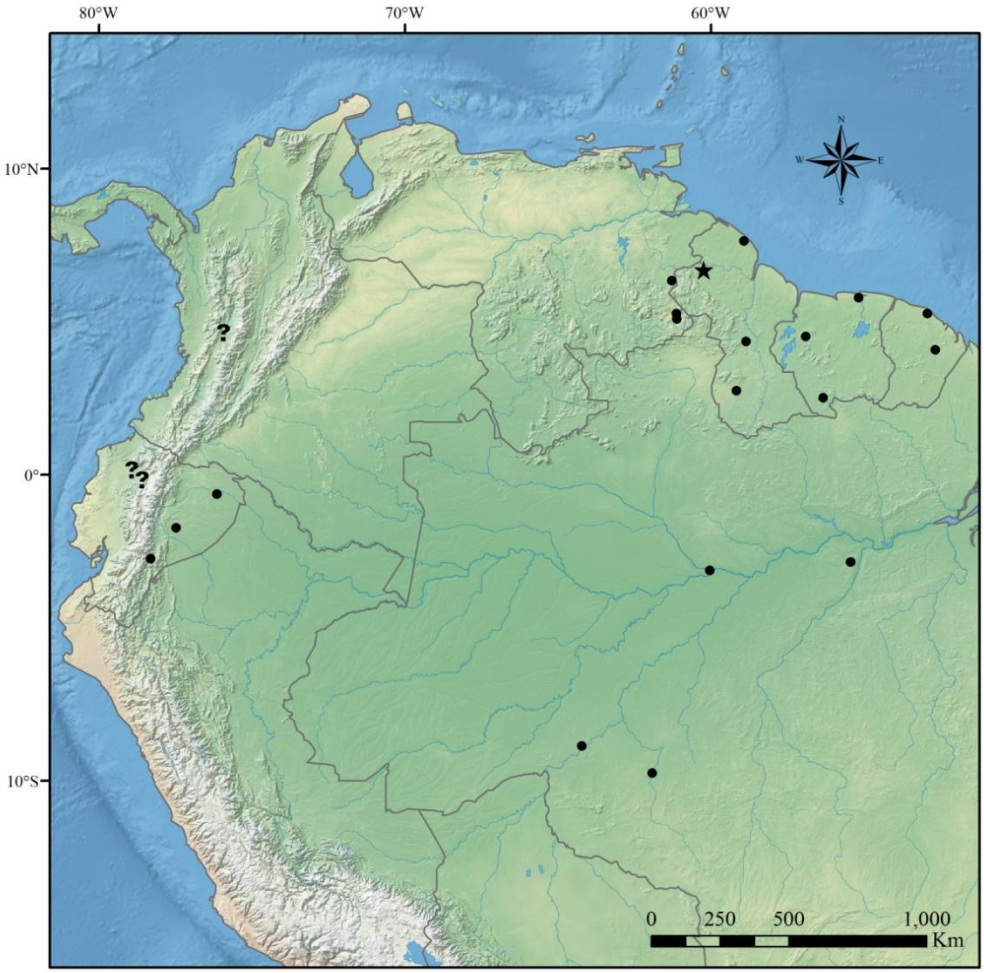

Figure 2. Distribution of *C. mastivus* in South America, including the type locality (star). The question marks represent the dubious localities on western side of the Andes.

EMENDED DIAGNOSIS: The largest *Cynomops* known (Males: FA 47.00–51.24, n=6; GLS 22.30–24.71, n=5; Females: FA 41.77–46 n=11; GLS 19.15–20.96 n=10; Table 5). Dorsal pelage is dark reddish brown, and the ventral coloration is uniformly brown, similar or slightly paler than dorsum; anterior face of lacrimal ridges form an abrupt angle with the forehead; nasal process of premaxilla are well developed, with the lateral margin of the external nares straight; the incisive foramina are located closer to the accessory foramen, the arrangement of the three foramina forming an equilateral triangle (Fig. 3A); basisphenoid pits are absent; there is a shallow fossa in the posterior squamosal bone, where the zygoma meets the braincase (see Velazco, 2005: 12); a large and shallow trigonid occurs on lower M1 (Fig. 4A); a well-developed median ridge on the lingual face of the second lower premolar is present; the lower first premolar measures two-thirds or more of the height of the second lower premolar.

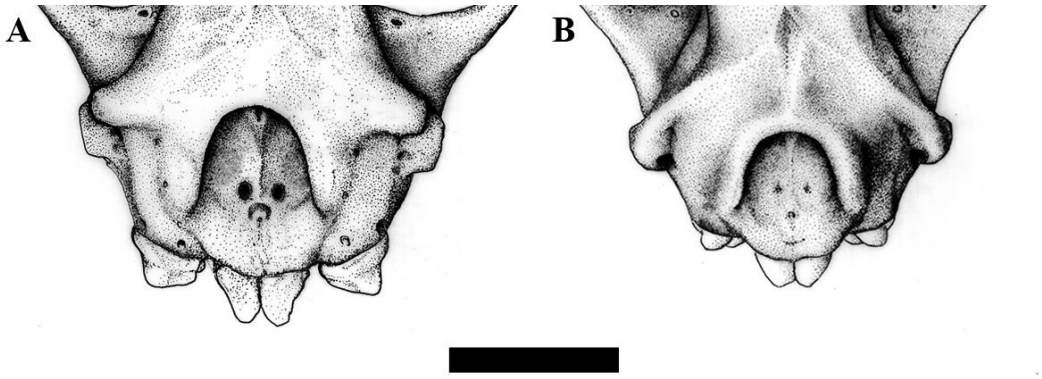

Figure 3. Configuration of the incisive foramina and accessory foramen in (A) *C. mastivus* (DZSJRP 11600; male) and (B) *C. abrasus* (DZSJRP 2162; male). Note that the accessory foramina is located relatively closest from the incisive foramina in *C. mastivus*, and farther in *C. abrasus*. Scale bar = 5 mm.

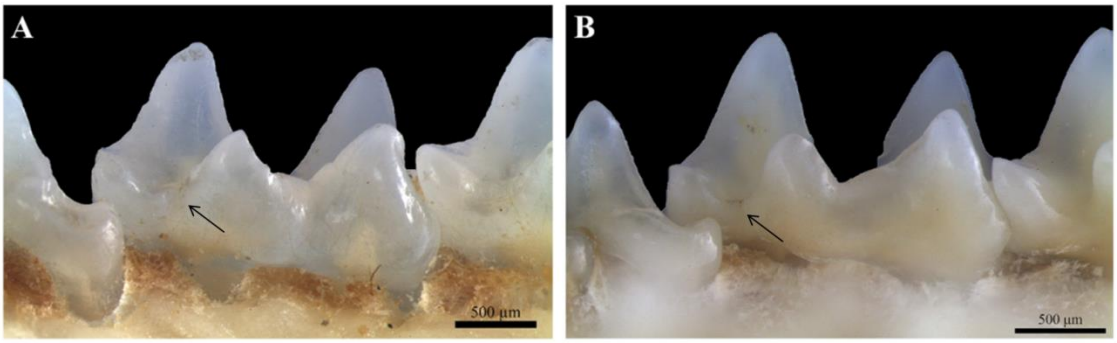

Figure 4. Lingual view of the first lower molar in (A) *Cynomops mastivus* (DZSJRP 11600; male) and (B) *C. abrasus* (DZSJRP 2162; male). Arrows indicate the trigonid. Note the shallow and wide trigonid in *C. mastivus*, and deep and narrow trigonid in *C. abrasus*.

Table 5. Measurements[a] (mm) of *Cynomops abrasus* and *C. mastivus* from several localities in South America (Appendix 1).

	Cynomops abrasus		*Cynomops mastivus*	
Number	38 females	20 males	11 females	06 males
Weight	31.50 (30.00, 33.00) 2	31	29.57 (27.00–33.00) 3	–
FA	44.51 (40.60–47.50) 35	45.84 (42.20–49.35)18	43.80 (41.77–46.00) 11	49.12 (47.00–51.24) 6
E*	17.83 (17.00–20.00) 6	19.00 (2)	18.40 (16.00–20.00) 5	17.00 (16.00–18.00) 2
TL*	35.46 (34.00–39.00) 14	38.00 (33.00–42.00) 7	35.30 (32.00–42.00) 10	41.50 (39.00–44.00) 2
HF*	11.54 (9.00–13.00) 13	11.80 (10.00–13.00) 5	12.20 (11.00–13.00) 10	10.29 (9.88–11.00) 3
GLS	19.59 (18.40–20.49) 37	21.01 (19.94–22.26) 12	20.08 (19.15–20.96) 10	23.35 (22.30–24.71) 5
POB	5.15 (4.74–5.72) 36	5.24 (4.99–5.56) 12	5.21 (4.97–5.40) 10	5.77 (5.51–6.29) 5
ROS	8.82 (8.05–9.68) 35	9.63 (8.63–10.23) 16	8.80 (8.43–9.20) 9	10.72 (10.16–11.31) 5
C-C	5.68 (5.19–6.24) 35	6.33 (5.94–6.78) 17	5.91 (5.63–6.15) 10	7.13 (6.64–7.88) 5
ZB	14.01 (12.93–14.56) 31	14.95 (14.29–15.85) 14	14.26 (13.85–14.93) 10	16.82 (16.05–17.9) 4
BB	9.99 (9.37–10.44) 37	10.22 (9.59–10.75) 17	10.12 (9.80–10.33) 10	10.98 (10.57–11.42) 5
MB	13.59 (12.44–14.40) 31	14.97 (13.93–16.21) 15	13.83 (12.90–14.48) 9	17.04 (15.58, 17.86) 3
MTRL	7.66 (7.10–8.16) 36	8.12 (7.45–8.61) 17	7.82 (7.36–8.13) 10	8.82 (8.64–9.06) 5
BM	9.60 (9.03–10.22) 37	9.95 (9.45–10.42) 16	9.63 (9.25–9.98) 10	10.46 (10.09–10.99) 5
CIL	19.80 (18.42–20.86) 35	21.19 (19.77–22.48) 17	20.33 (19.38–21.39) 10	23.63 (22.95–24.91) 5
ML	14.88 (13.89–15.64) 37	15.80 (14.71–16.68) 17	15.31 (14.81–15.77) 10	17.52 (16.61–18.23) 5

[a]Summary statistics (mean, range, and sample size) of measurements for each species.
*Measurements taken from the labels.

REDESCRIPTION: *Cynomops mastivus* is the largest species of *Cynomops* (Table 5). The dorsal pelage coloration is dark-chocolate-brown, with a uniformly colored venter,

slightly paler than the dorsum. The pelage is silky, but the dorsal fur is not very long (4 mm in length, taken on the level of the scapular area), and the individual dorsal hairs are bicolored, with the basal third of each colored pale-buff.

The face is blackish and virtually naked; the upper lip and the dorsal border of the narial region are smooth; the triangular and blackish ears are slightly separated each other at the forehead (space $\leq$ 4.0 mm); the patagium, feet and tail are also blackish; the propatagium is narrow, and the posterior plagiopatagium is inserted lateral to the base of the feet. There is dark-chocolate-brown fur distributed along one-third of the forearm, and along the adjacent propatagium. A second patch of fur extends from the posterodorsal surface of the distal plagiopatagium, next to the wrist, to dactilopatagium IV.

The skull is robust, with the sagittal and the occipital crests consistently well developed in males; the anterior face of the lacrimal ridges forms an abrupt angle with the forehead (Fig. 5A, B); the nasal process of the premaxilla is well-developed, with the lateral margin of the external nare straight, particularly in males, and less markedly in females (Fig. 6A), and the incisive foramina are located relatively close to the accessory foramen (Fig. 3A).

The basisphenoid pits are absent; there is a shallow fossa on the posterior squamosal bone, where the zygoma meets the braincase (see Velazco, 2005: 12). There is a massive mandible in males, with a concave corpus along its length (Fig 5B). There is a large, and shallow trigonid on the lower M1 (Fig. 4A), and a well-developed median ridge on the lingual face of the second lower premolar, and the first lower premolar is two-thirds or more of the height of the second lower premolar.

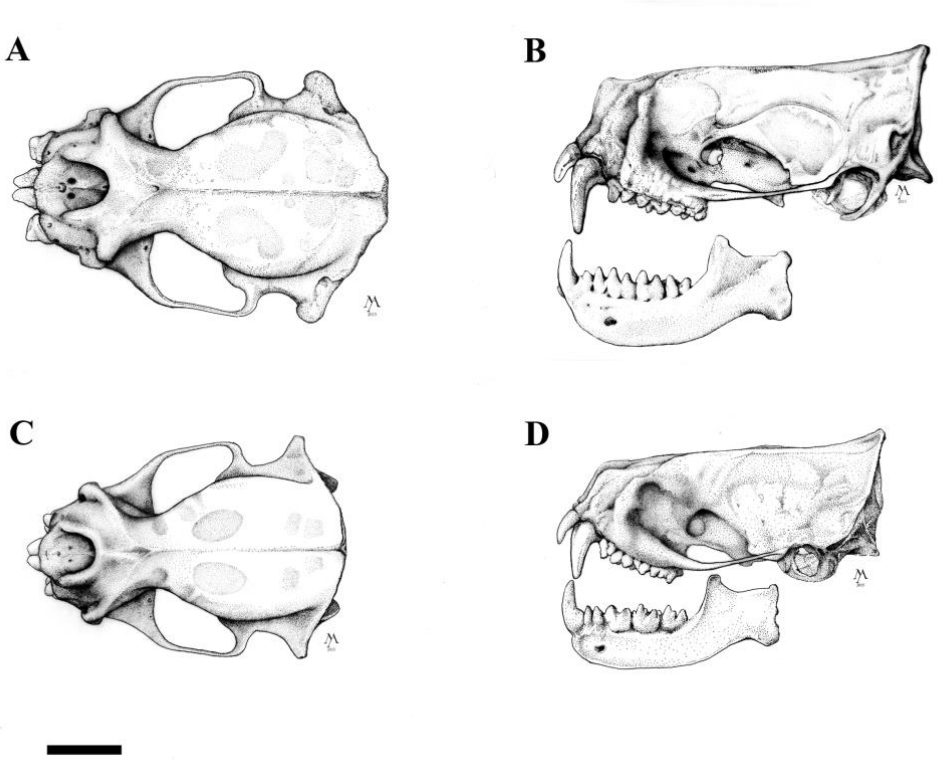

Figure 5. Dorsal and lateral view of (A, B) *Cynomops mastivus* (DZSJRP 11600; male) and, (C, D) *C. abrasus* (DZSJRP 2162; male). Scale bar = 5 mm.

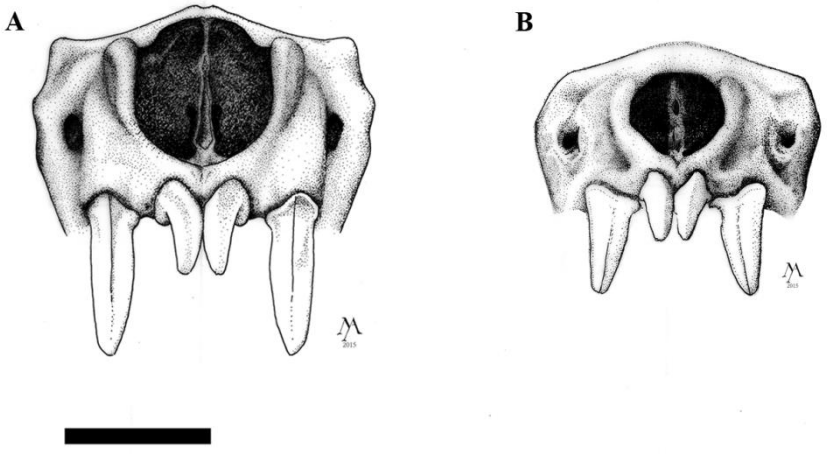

Figure 6. Rostral view of (A) *C. mastivus* (DZSJRP 11600; male) and (B).*C. abrasus* (DZSJRP 2162; male). Note the well-developed nasal process of premaxilla, with the lateral margin of the external nares straight in *C. mastivus*, and the reduced nasal process with lateral margin of the external nares concave in *C. abrasus*. Scale bar = 5 mm.

COMPARISONS: *Cynomops mastivus* can be readily distinguished from all the other species of the genus (*C. abrasus*, *C. greenhalli*, *C. milleri*, *C. paranus*, and *C. planirostris*) by its large size (Table 5), and by the consistently well-developed posterior sagittal and occipital crests in males. *Cynomops mastivus* resembles *C. abrasus*, and both can be distinguished from the small-median species of *Cynomops* (*C.greenhalli*, *C. milleri*, *C. paranus* and *C. planirostris*) by their larger size, with males and females having forearm lengths measuring more than 42mm and 40mm, respectively, while males and females of smaller *Cynomops* have forearm lengths measuring less than 40mm and 39 mm, respectively). *Cynomops mastivus* and *C. abrasus* can also be separated from smaller forms of *Cynomops* by patterns of the ventral pelage coloration, which is only slightly lighter than the dorsum in the two larger forms and may be much paler in the smaller species, at least in part of the ventral axis of the body.

Cynomops mastivus can be distinguished from *C. abrasus* by the presence of a shallow and wide trigonid on the lower M1, which is deep and narrow in *C. abrasus*; by the anterior face of lacrimal ridges that forms an abrupt angle with the forehead in *mastivus*, and slopes smoothly to the forehead in *C. abrasus*; by the massive and concave mandible of the males of *mastivus*, as opposed to the gracile and relatively straight, not concave, mandible of *C. abrasus*, and by the larger and more robust skull of *mastivus* (Table 5; Fig. 5).

4. Discussion

The diversity of *Cynomops* has been underestimated for decades, with several lineages likely to be uncovered and described in the near future, allowing us to begin understanding the evolutionary history of these unique Neotropical molossids. The

monophyly of *Cynomops* and its sister relationship with *Molossops* recovered by our analysis is consistent with the phylogenetic hypothesis of Peters *et al*. (2002) based on restriction enzymes of mtDNA, and of Ammerman *et al*. (2012) based on four genes. However, the morphological data of Gregorin and Cirranello (2015) indicate a basal position for *Cynomops* in a clade composed by *Molossops*, *Neoplatymops*, *Platymops*, *Sauromys* and *Mormopterus*, or a sister group relationship between *Cynomops* and a clade that contains *Myopterus*, *Cheiromeles*, *Molossus*, and *Promops*. As we have not included all the content of molossids as did Ammerman *et al*. (2012) and Gregorin and Cirranello (2015) we have only a partial test for the placement of *Cynomops* in the Molossidae tree. Moreover this question remains contentious because of the different hypotheses pointed by molecular (Ammerman *et al*., 2012) and morphological data (Gregorin and Cirranello, 2015).

According to our analysis, a total of seven morphological characters support the clade of *Molossops* and *Cynomops*, and four synapomorphies support the monophyly of *Cynomops*. *Cynomops* can be differentiated from *Molossops* by several characters, including the distance separating the insertion of the ears in the head (> 4.0 mm in *Molossops*), the presence of two lower incisors in each hemimaxilla (one in *Molossops*), the pattern of shallow basisphenoid pits in the basisphenoid bone (deep pits in *Molossops*) and the absence of a premetacrista on the M3 (medially developed in *Molossops*) (Thomas, 1920; Williams and Genoways, 1980; Eger, 2008; see Table 1 and Appendix C). Karyological characters including diploid and fundamental numbers and chromosome morphology differentiating *Cynomops* and *Molossops* have also been reported (Gardner, 1977; Morielle-Versute *et al*., 1996).

Our phylogeny overall agreed with that of Peters *et al*. (2002) in recovering four main clades within the *Cynomops* tree. We however uncovered three additional lineages: *C. abrasus* (Brazil, Paraguay and Peru), *Cynomops* sp.1 (Panama) and *Cynomops* sp.2 (eastern Ecuador). The position of *C. planirostris* is still conflicting; Peters *et al*. (2002) recovered moderate support for sister relationships between *C. planirostris* and *C. paranus*, and considered *C. paranus* a separate taxon from *planirostris*. In contrast, our results suggested a basal position for *C. planirostris* (clade B) to all the other species of *Cynomops*, with the exception of *C. mexicanus* and *Cynomops* sp. 1.

Strict relationships between *C. mastivus* and *C. greenhalli* were strongly supported, indicating that *C. mastivus* is closer to *C. greenhalli* than to *C. abrasus*, which in turn is basal to the *greenhalli* + *abrasus* clade .Warner *et al*. (1974) did not find differences between the karyotypes of *C. abrasus* from southeastern Peru and *C. greenhalli*, but the authors examined a single individual of *C. abrasus*, and there is no published karyological data available for *C. mastivus* (Santos *et al*., 2001; Leite-Silva *et al*., 2003). More recently, techniques such as banding and fluorescent *in situ* hybridization have showed that there are differences in number of NOR-bearing chromosomes in *Cynomops*, with *C. abrasus* having NORs in five (11, 12, 14, 15 and 16) pairs of chromosomes (Morielle-Versute *et al*., 1996), while *C. planirostris* have NORs located only in two pairs (9 and 10) (Leite-Silva *et al*., 2003).

Although the mean *p*-distances observed among allopatric haplogroups of *C. planirostris*, *C. abrasus*, and *C. greenhalli* (in this case among haplotypes) were slightly higher than the threshold suggested by Bradley and Baker (2001) for the intraspecific variation of mammals, we did not yet find morphological variation apparent from the systems commonly analyzed (e.g. skull, tooth) between the individuals of each haplogroup.

Therefore, it merits further investigation on morphological systems rarely analyzed (e.g. postcrania, myology, glans penis) and phylogeographic analyses with denser geographic sampling and employing nuclear genes (to consider paternal inheritance either) to clarify whether they represent conspecific populations or cryptic taxa (e.g. Clare, 2011).

Cynomops milleri has a confused taxonomic history, treated as a subspecies of *C. planirostris* (Koopman, 1978), synonymized with *C. paranus* (Simmons and Voss, 1998), and treated as a distinct species by Eger (2008). The paraphyletic group formed by *C. milleri* and *C. paranus*, allied to the low genetic distance detected between these taxa require further examination, including comparisons with holotypes in order to elucidate the status of these two taxa.

Recent systematic revisions of Neotropical bats taxa have showed that widespread taxa often correspond to species complexes, and many new species have been described over the last decade (e.g. Velazco and Patterson, 2008; Velazco *et al*., 2010; Velazco and Patterson, 2014; Tavares *et al*., 2014). The evidences obtained in the present study revealed that *Cynomops* may be a complex of eight species. One of the putative new forms, *Cynomops* sp. 1, is represented by nine specimens from Panama separated by high mean p-distances (7.9 – 12.5%) from the remaining species. The other putative species, *Cynomops* sp. 2, encompasses five specimens from eastern side of Andes, in Ecuador, and mean p-distances between this form and the other *Cynomops* varied from 4.6 to 12.5%. Those samples have been previously identified as *C. paranus* (Simmons and Voss, 1998; Reid *et al*., 2000; Peters *et al*., 2002; Eger, 2008) delimiting an equivocal broad distribution for *C. paranus* from Panama to Argentina (Eger, 2008).

Regarding the nomenclature terrain, *Dysopes abrasus* has historically been mistakenly included in the genus *Eumops* (Husson, 1962; Carter and Dolan, 1978).

However, Husson (1962) provided a detailed description of the *Dysopes abrasus* type, and demonstrated that it is actually an adult female of *Molossops*. The name *Dysopes abrasus* Temminck is therefore a senior synonym of *Molossops brachymeles* (Peters, 1865) and the correct name applied to the species is *Cynomops abrasus* (Temminck, 1827).

Cabrera (1958) suggested that the morphological variation between the forms of *Cynomops abrasus* was not enough to separate them as distinct species, but instead they could be recognized as "geographical races". In fact, many authors have commented the similarities in size of *C. abrasus*, *C. a. brachymeles* and *C. a. cerastes*, suggesting that additional material was necessary to confirm their taxonomic status (Sanborn, 1932; Husson, 1962; Eger, 2008). In contrast, the larger size, darker coloration, and other cranial characters related to the robustness of the skull were evidences long claimed as supporting the status of *C. a. mastivus* as a separate species (Husson, 1962; Uieda and Taddei, 1980; Eger, 2008). In agreement with those statements, our morphological and molecular evidences allowed us to recognize two species inside the pool of individuals previously under the name *C. abrasus*: the type-nominal *C. abrasus* from several localities in South America, widespread distributed from Peru to Argentina and including the type locality in state of São Paulo, Brazil (Eger, 2008), and *C. mastivus* inhabiting Amazonian lowlands in the Guiana Shield, Ecuador and Brazil (Fig. 2).

Alberico and Naranjo (1982) reported three individuals of *C. abrasus* from southwestern Colombia (2 males and 1 female), but the measurements of both males do not fit the expected variation for *C. mastivus*. Another two records from the western Andes in Ecuador were reported by Tirira (2012). A single specimen from western Andes of Colombia (FMNH 89574) that we were able to analyze is broken, hindering the correct

identification. Therefore, a revision of the material of large-sized *Cynomops* from the west side of Andes is necessary.

Mitochondrial markers have been exceptionally useful for testing morphology-based taxonomy and detecting possible cryptic species in bats (e.g., Mayer and von Helversen, 2001; McDonough *et al*., 2008; Larsen *et al*., 2011; Siles *et al*., 2013; and this paper). The morphological characters herein employed have concurrently improve the support of the nodes recovered, and the understanding of the evolution of the genus, emphasizing the importance of using multiple approaches for phylogenetic studies (Nixon and Carpenter, 1996; Nylander *et al*., 2004; Giannini and Simmons, 2005).

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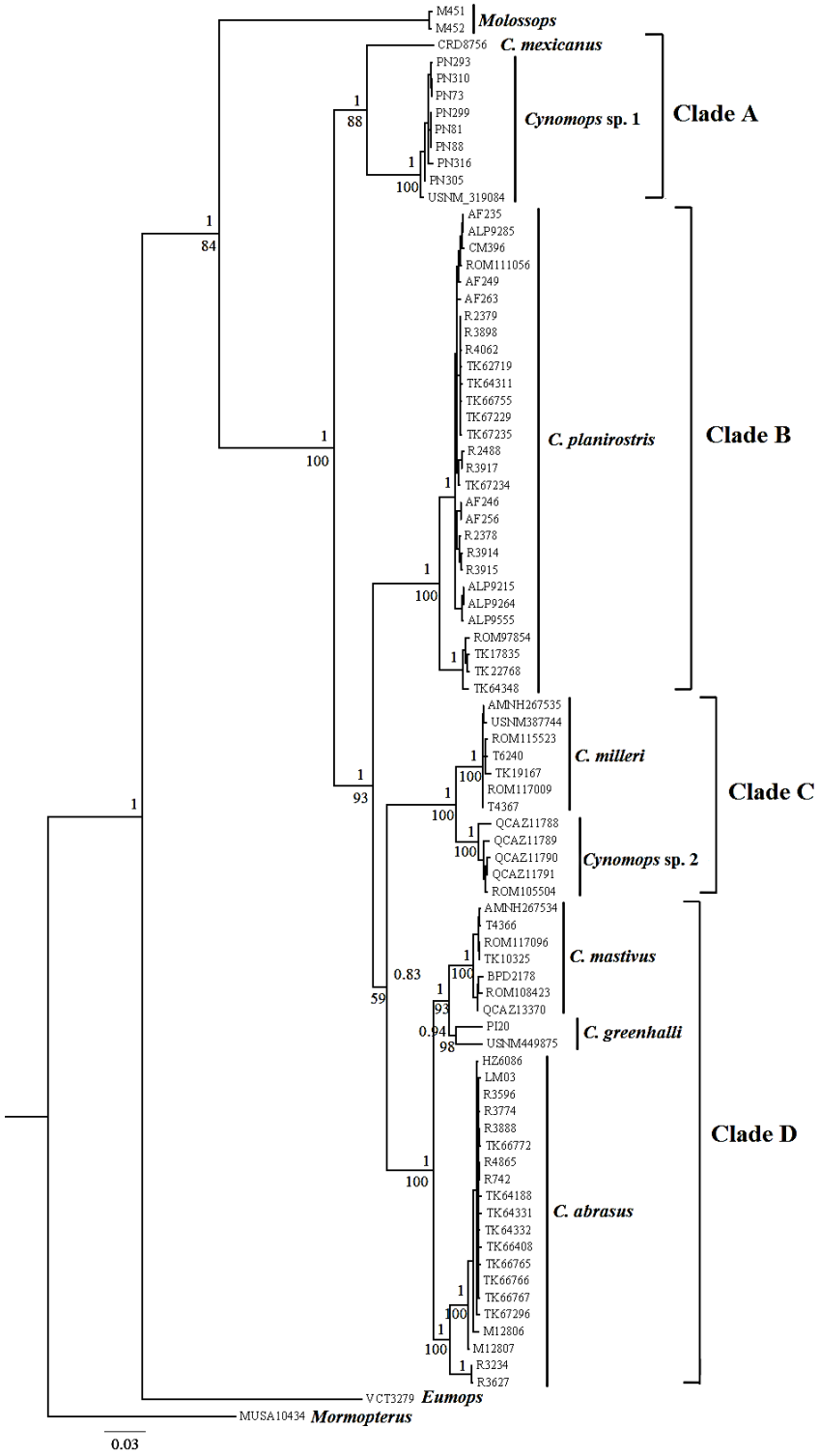
SUPPLEMENTARY INFORMATION



Supplementary information, Figure 1. Bayesian tree of *Cynomops* species generated with 2497 base pairs of the mtDNA (COI + Cyt *b*). Values above branches represent Bayesian posterior probabilities (PP) and below branches, the maximum-likelihood (ML) bootstrap. See Appendix B for museum acronyms and collection sites.

Appendix A. Examined material: ♂ = male, ♀ = female.

Cynomops planirostris (total 141) – **Guyana**: BERBICE: USNM86907 (♂); EAST DEMERARA-WEST COAST BERBICE: Rio Cuyuni, Hyde Park: FMNH22486 (♂), 22487 (♂); UPPER TAKUTU-UPPER ESSEQUIBO, RUPUNINI: Ruawau River, Raa Wau: ROM37955 (♂), 38551 (♀); Warimure, Weri More, Quash Wau Area, 12 mi NE Dadanawa: ROM44426 (♂), 52235(♂); Kataliriwau River, Katalier Wau, 20 mi E of Dadanawa: ROM65368 (♂); Kuitaro River, 30 mi E of Dadanawa: ROM71677 (♀); Kuma River, 5 mi E, 5.5 mi S of Lethem, Kanuku Mountain: ROM97854 (♀). **Colombia**: AMAZONAS: Letícia: ROM70999 (♀), 62577 (♂); BOYACA: Pore: ROM62520 (♂). **Venezuela**: APURE: San Fernando De Apure: USNM374031 (♂). BOLIVAR: Hato La Florida, 47 Km ESE Caicara: USNM405830 (♀); 2km NE Maripa: KU119090 (♂). AMAZONAS: San Juan, 163 Km ESE Pto. Ayacucho, Rio Manapiare: USNM409498 (♀), 409499 (♀), 409501 (♀), 409503 (♀), 409504 (♀), 409505 (♀), 409508 (♀), 409509 (♂), 409511 (♂), 409512 (♀), 409513 (♀), 409514 (♀), 409515 (♂), 409516 (♀), 409517 (♀), 409518(♀), 409519 (♀), 409522 (♀), 409524 (♀), 409525 (♀), 409552 (♀), 409553 (♀), 409554 (♀), 409555 (♂), 409556 (♂), 409557 (♀), 409558 (♀), 409559 (♀), 409561 (♂), 409562 (♂), 409563 (♂), 409564 (♀), 409565 (♂), 409566 (♂), 418382 (♀), 418384 (♀), 418387 (♀), 418388 (♀), 418398 (♀), 418402 (♀), 418406 (♀), 418407 (♀), 418408 (♀), 418409 (♀), 418410 (♀), 418411 (♀), 418414 (♀), 418416 (♀), 418417 (♀), 418418 (♀), 418419 (♀), 418420 (♀), 418421 (♀); San Carlos De Rio Negro: USNM560638 (♂), 560639 (♂), 560640 (♀), 560641 (♀), 560687 (♂), 560688 (♀), 560689 (♀). MONAGAS: Hato Mata De Bejuco, 55 Km SSE Maturin: USNM441842 (♀), 441843 (♀), 441844 (♂), 441845 (♀), 441846 (♀). BOLIVAR: Maripa, Sucre: AMNH17096 (♀), 17097 (♀). **Bolivia**: BENI: San Joaquin: FMNH96038 (♀). SANTA CRUZ: Chiquitos, Robore: AMNH260261 (♂). **Brazil**: SÃO PAULO: Sales, Fazenda Esplanada: ROM77311 (♂); Estação Ecológica de Caetetus: ROM111056 (♀); Urupês: AMNH236221 (♂). MATO GROSSO: Serra do Roncador, 264 Km N Xavantina: USNM393768 (♂). MATO GROSSO DO SUL: Urucum: FMNH26772 (♂). MARANHÃO: Buriti: AMNH37043 (♀), 37049 (♀). PERNAMBUCO: Estação Ecológica do Tapacura, São Lourenco da Mata: USNM555727 (♂). AMAZONAS: Tefé: USNM531145 (♀); Rio Negro, Miripinima, Airo: AMNH79731 (♀), 79733 (♀); Rio Madeira, Rosarinho: AMNH92254 (♀); Vila Bela, Imperatriz, Parintins: AMNH92971 (♂); Rio Amazonas, Itacoatiara: FMNH20640 (♀), 20649 (♂), 20650 (♀). PARÁ: Rio Tapajós, Igarapé Brabo: AMNH94642 (♀), 94644 (♀), 94646 (♂), 94648 (♂), 94649 (♀), 94650 (♀), 94652 (♂), 94653 (♀); Rio Tapajós, Aramanay: AMNH94633 (♀), 94636 (♀); Rio Tapajós, Caxiricatuba: AMNH94639 (♂), 94640 (♂); Rio Amazonas, Faro: AMNH93879 (♂), 93880 (♀), 93882 (♀), 93883 (♀), 93886 (♂). PARÁ: Santarém: MZUSP13892 (♀); Santarém, Vila Alter do Chão: INPA3935 (♂), 3959 (♀), 3960(♀); Rio Tapajós, Fordlandia: MZUSP17589 (♀). RONDÔNIA: Vila Veneza: INPA6005 (♂), 6006 (♀), 6007 (♀), 6008 (♀). **Paraguay**: ALTO PARAGUAI: Fuerte Olimpo: AMNH234455 (♀), 234456 (♂), 234457 (♂), 234458 (♀), 234459 (♀); Estancia Guyra Toro: TTU116566 (♀). CORDILLERA: Juan de Mena:

USNM552738 (♀). CANINDEYU: Reserva Natural del Bosque Maracayu: TTU116561 (♀). CONCEPCIÓN: Parque Nacional Serrania de San Luis: TTU80261 (♀). MISIONES: Refugio Yabebyry-Sta. Ana: TTU80330 (♂), 80331 (♀). NEEMBUCO: Estancia Yacare: TTU80591 (♀). PRESIDENTE HAYES: Estancia Samaklay: TTU80500 (♀). BOQUERÓN: Base Naval Pedro P. Peña: TTU79997 (♀).

Cynomops paranus (total 38) – **Panama**: PANAMA: Pacora: USNM319084 (♀), 319085 (♀), 319086 (♀), 319087 (♀), 319088 (♀); Ciudad de Panamá: AMNH183161 (♀). CANAL ZONE: Fort Clayton: USNM317627 (♀), AMNH183865 (♀); Miraflores Locks: USNM312114 (♀); Balboa, La Boca: AMNH183160 (♂), 183163 (♀); Cocoli: AMNH183168 (♂).**Colombia**: NORTE DE SANTANDER: Cucuta: FMNH51450 (♂), 51451 (♂), 51452 (♂). PUTUMAYO: Mocoa: ROM41479 (♂). **Venezuela**: BOLÍVAR: El Manaco: USNM387745 (♂). **French Guiana**: PARACOU: Near Sinnamary: AMNH267535 (♂); SAUL: KU135372 (♂), 13373 (♀), 135374 (♀), 135375 (♀).**Guyana**: UPPER DEMERARA-BERBICE: Arampa, 3 mi S of Ituni: ROM57375 (♂), 57337 (♀),57505 (♀). POTARO-SIPARUNI: 38 Mile Camp, 35 km SW of Kurupukari, Iwokrama Reserve: ROM108465 (♀), 108466 (♀); 's' Falls, Siparuni River, 50 km Wsw of Kurupukari, Iwokrama Reserve: ROM109178 (♀). ESSEQUIBO ISLANDS-WEST DEMERARA: Shanklands: ROM115522 (♂), 115523 (♂), 115524 (♀), 115525 (♀), 115579 (♀). **Suriname**: SIPALIWINI: Bakhuis: ROM117009 (♀), 117097 (♂). **Brazil**: MATO GROSSO: Serra Do Roncador, 264 Km N Xavantina: USNM393769 (♂). AMAZONAS: Manaus, Rio Negro, Igarapé Cacao Pereira: AMNH79745 (♀). PARÁ: Santarém, Alter do Chão: INPA3958 (♂).

Cynomops milleri (total 2): **Peru**: LORETO: Yurimaguas: FMNH19652 (♀). **Venezuela**: BOLÍVAR: El Manaco, 59Km SE El Dorado, Km74: USNM387744 (♀).

Cynomops greenhalli (total 29) – **Panama**: DARIEN: Tacarcuna Village Camp: USNM310264 (♂), 310265 (♀), 310266 (♂), 310267 (♀), 310268 (♀), 310269 (♀), 310270 (♀), 310271 (♀), 310272 (♀), 310273 (♂), 310274 (♀), 310275 (♂); Jaque, Rio Imamadol: USNM363108 (♀). CANAL ZONE: Fort Amador: USNM396481 (♂). BOCAS DEL TORO: Isla San Cristobal: USNM449875 (♂). **Belize**: AMNH274123 (♂). **Colombia**: CUNDINAMARCA: Girardot: ROM54534 (♀); Melgar: ROM65474 (♂). **Venezuela**: ARAGUA: Ocumare de la Costa, 3km S: USNM510579 (♂). SUCRE: Tacal, 1Km SSW Cumana: KU119087 (♀), 119088 (♀). **Trinidad and Tobago**: TRINIDAD: Saint George County, Port of Spain: AMNH175326 (♂), 176285 (♀), 176286 (♀), 207071 (♀). **Ecuador**: LOJA: Zapotillo, Via Paletillas: QCAZ3334 (♀).GUAYAQUIL: Bosque Protector Cerro Blanco: LEOCAN243 (♂), 244 (♀). **Brazil**: AMAZONAS: Rio Preto da Eva, Reserva Galvão: INPA2658 (♂).

Cynomops mexicanus (total 7) – **Mexico**: JALISCO: 7 1/2mi SE, tecomates, 1500ft: KU108609 (♂), 108610 (♀), 111621 (♂). GUERRERO: Chilpancingo, 3 Km N Agua del

Obispo: KU99741 (♀). OAXACA: 20 mi S, 5mi E Sola de Veja, 4800 ft: KU99747 (♀). NAYARIT: El Casco, Rio Chilte: USNM511544 (♀); Arroyo De Jiguite, Rio Santiago: USNM523453 (♀).

Cynomops abrasus (total 57) – **Paraguay**: USNM8256 (♀). PARAGUARI: Sapucay: USNM114902 (♂), 114925 (♀), 114926 (♂), 114927 (♀), 114928 (♀), 114929 (♂), 114931 (♀), 114934 (♀), 114937 (♀), 116785 (♀), AMNH23800 (♀), 23801 (♂), FMNH48781 (♀), 48777 (♀), 48780 (♀), 48779 (♀). DEPARTAMENTO CENTRAL: San Lorenzo: USNM461896. GUAIRÁ: Vilarrica: BMNH 1.8.1.13 (♂), AMNH239235 (♂). CANINDEYU: Reserva Natural del Bosque Mbaracayú: TTU116562 (♀), 116563 (♂), 116564 (♂). CONCEPCIÓN: Parque Nacional Serrania de San Luis: TTU80244 (♀), 80245 (♀), 80260 (♀). ALTO PARAGUAY: Estancia Punto Alto: TTU116568 (♀). MISSIONES: Refugio Yabebyry-Sta. Ana: TTU80329 (♀). NEEMBUCO: Estancia Yacare: TTU80589 (♂), 80590 (♀). **Brazil**: MATO GROSSO: 50Km São Domingos, Rio das Mortes: MZUSP15655 (♂). MINAS GERAIS: Salinas: CP14 (♀). SÃO PAULO: USNM141441 (♀); Nova Granada: AMNH 236220 (♀), DZSJRP11670 (♂), 11665 (♀); Nipoã: DZSJRP2162 (♂); Mirassol: DZSJRP4807 (♂); São Vicente: MZUSP26711; Votuporanga: DZSJRP3178 (♀), 3179 (♀). PARANÁ: Maringá: DZSJRP10456 (♀), 10457 (♂); Itambé: DZSJRP10540 (♀). RIO DE JANEIRO: LDM 515 (♀), 590 (♂), 712 (♀), 714 (♂), 716 (♀), 765 (♀), 766 (♂), 767 (♀), 1414 (♀). MARANHÃO: Barra do Corda: MZUSP7937 (♂). PIAUÍ: Valença, Fazenda Olhos d'água: USNM555724 (♀), 555725 (♀). MATO GROSSO: Serra do Roncador, 280 Km N Xavantina: USNM393767 (♂).

Cynomops mastivus (total 18): **Guyana**: CUYUNI-MAZARUNI: Bartica Grove, lower Essequibo: BMNH 10.11.10.3 (♂). UPPER TAKUTU-UPPER ESSEQUIBO: Marurawaunawa Village, Machawira, Behind Maruranowa: ROM35637 (♂). BARIMA-WAINI, NORTH WEST: Akwero, Cart Market, 1 mi E de Aquero: ROM67507 (♂). POTARO-SIPARUNI: Iwokrama Reserve, 38 Mile Camp, 35 km SW of Kurupukari: ROM108423 (♀). **French Guiana**: CAYENNE: Sinnamary, Paracou: AMNH267534 (♀). **Suriname**: SIPALIWINI: Alalapadu, North of Sipaliwini River: ROM39498 (♀). Bakhuis: ROM117096 (♀).**Venezuela**: BOLÍVAR: El Manaco, 59 Km SE El Dorado, Km 74: USNM387743 (♀).**Colombia**: NARIÑO: Candelilla: FMNH89574 (♂). **Ecuador**: ORELLANA: Ononaco, Bloque 16, Km 110, Puente del Río dícaro: QCAZ13370 (♂), 13371 (♀). **Brazil**: RONDÔNIA: Porto Velho, Vila Veneza: INPA6004 (♂). AMAZONAS: Manaus, Bairro do Coroado: DZSJRP11600 (♂). PARÁ: Rio Tapajós, Igarapé Brabo: AMNH94624 – 28 (♀).

Appendix B. Locality, catalog/tissue numbers for the sequences used in this study.

Taxon	Locality	Catalog no./ tissue no.
C. a. mativus	French Guiana: Cayenne	AMNH267534
C. a. mastivus	Guyana: Potaro-Siparuni	ROM108423
C. a. mastivus	Suriname: Sipaliwini	ROM117096
C. a. mastivus	French Guiana: Nouragues	T4366
C. a. mastivus	Suriname: Nickerie	TK10325
C. a. mastivus	Equador: Orellana	QCAZ13370
C. a. brachymeles	Peru: Madre de Dios	M12806
C. a. brachymeles	Peru: Madre de Dios	M12807
C. a. brachymeles	Peru: Madre de Dios	HZ6086
C. a. mastivus	Brazil: Rondônia	BDP2178
C. a. abrasus	Brazil: Minas Gerais	LM03
C. a. abrasus	Brazil: São Paulo, SP	UFMG3566/ R3234
C. a. abrasus	Brazil: SJR Preto,SP	UFMG4122/ R3596
C. a. abrasus	Brazil: Piracicaba, SP	UFMG3564/ R3627
C. a. abrasus	Brazil: SJR Preto,SP	UFMG3567/ R3774
C. a. abrasus	Brazil: SJR Preto,SP	UFMG3568/ R3888
C. a. abrasus	Brazil: SJR Preto,SP	UFMG4123/ R4865
C. a. abrasus	Brazil: SJR Preto,SP	UFMG3565/ R742
C. a. cerastes	Paraguay: Concepción	TTU80244/ TK64188
C. a. cerastes	Paraguay: Ñeembucu	TK64331
C. a. cerastes	Paraguay: Ñeembucu	TK64332
C. a. cerastes	Paraguay: Itapúa	TK66408

C. a. cerastes	Paraguay: Canindeyu	TTU116562/TK66765
C. a. cerastes	Paraguay: Canindeyu	TK66766
C. a. cerastes	Paraguay: Canindeyu	TK66767
C. a. cerastes	Paraguay: Canindeyu	TK66772
C. a. cerastes	Paraguay: Alto Paraguay	TTU116568/TK67296
C. greenhalli	Panama: Bocas Del Toro	USNM449875
C. greenhalli	Ecuador: Guayaquil	LEOCAN243
C. mexicanus	Mexico: Nayarit	CRD8756
C. milleri	Venezuela: El manaco	USNM387744
C. paranus	French Guiana: Cayenne	AMNH267535
C. paranus	Guyana: Essequibo Islands	ROM115523
C. paranus	Suriname: Sipaliwini	ROM117009
C. paranus	French Guiana: Nouragues	T4367
C. paranus	French Guiana: Trinité - Aya	T6240
C. paranus	Venezuela: Bolivar	TK19167
C. planirostris	Guyana: Upper Takutu-Upper Essequibo	ROM97854
C. planirostris	Suriname: Nickerie	TK17835
C. planirostris	Peru: Huanuco	TK22768
C. planirostris	Brazil: Minas Gerais	CM396
C. planirostris	Brazil: Piracicaba, SP	UFMG3555/ R2378
C. planirostris	Brazil: Piracicaba, SP	UFMG3556/ R2379
C. planirostris	Brazil: Sorocaba, SP	UFMG3557/ R2488
C. planirostris	Brazil: Piracicaba, SP	UFMG3559/ R3898
C. planirostris	Brazil: Jundiaí, SP	UFMG3560/ R3914
C. planirostris	Brazil: Jundiaí, SP	UFMG3561/ R3915

C. planirostris	Brazil: Jundiaí, SP	UFMG3562/ R3917
C. planirostris	Brazil: Jundiaí, SP	UFMG3563/ R4062
C. planirostris	Brazil: São Paulo	ROM111056
C. planirostris	Brazil: Espírito Santo	ALP9215
C. planirostris	Brazil: Espírito Santo	ALP9264
C. planirostris	Brazil: Espírito Santo	ALP9285
C. planirostris	Brazil: Espírito Santo	ALP9555
C. planirostris	Brazil: Bahia	UFPB6485/AF246
C. planirostris	Brazil: Bahia	UFPB6505/ AF249
C. planirostris	Brazil: Bahia	UFPB6517/ AF256
C. planirostris	Brazil: Bahia	UFPB6500/ AF263
C. planirostris	Paraguai: Presidente Hayes	TK62719
C. planirostris	Paraguai: Concepción	TK64311
C. planirostris	Paraguai: Ñeembucu	TK64348
C. planirostris	Paraguai: Canindeyu	TTU116561/TK66755
C. planirostris	Paraguai: Alto Paraguay	TK67229
C. planirostris	Paraguai: Alto Paraguay	TK67234
C. planirostris	Paraguai: Alto Paraguay	TK67235
Cynomops sp. 1	Panama: Colon	PN73B
Cynomops sp. 1	Panama: Colon	PN81
Cynomops sp. 1	Panama: Colon	PN88
Cynomops sp. 1	Panama: Colon	PN293
Cynomops sp. 1	Panama: Colon	PN299
Cynomops sp. 1	Panama: Colon	PN305
Cynomops sp. 1	Panama: Colon	PN310

Cynomops sp. 1	Panama: Colon	PN316
Cynomops sp. 1	Panama: Pacora	USNM319084
Cynomops sp. 2	Ecuador: Nareno	QCAZ11788
Cynomops sp. 2	Ecuador: Nareno	QCAZ11789
Cynomops sp. 2	Ecuador: Nareno	QCAZ11790
Cynomops sp. 2	Ecuador: Nareno	QCAZ11791
Cynomops sp. 2	Ecuador: Napo	ROM105504
M. temminckii	Brazil: Minas Gerais	M451
M. temminckii	Brazil: Minas Gerais	M452
M. kalinowskii	Peru: Moquegua	MUSA10434
E. auripendulus	Brazil: Pará	VCT3279

Appendix C. Description of the morphological characters.

Body, facial and pelage morphology

Character 01: Dorsal border of the external nares

Dorsal margin of the nose surrounded by small, and obtuse warts (0), or smooth (1). The dorsal margin of the nose of *Cynomops* and *Eumops* is smooth, lacking warts and small hairs. In contrast, the dorsal margin of the nose is surrounded by small and obtuse warts in *Molossops* and *Mormopterus*. This character was previously used by Gregorin (2009: character 1).

Character 02: Upper lips

Upper lips wrinkled (0), or smooth (1). *Cynomops*, *Eumops* and *Molossops have* smooth upper lips, while *Mormopterus* have it slightly wrinkled. This character was previously used by Gregorin (2009: character 9).

Character 03: Insertion of the ears at the forehead

Anterodorsal ear pinnae joined in a common point at forehead (0), or ears separated by a small space equal or less than 4.0 mm (1), or separated by a space more than 4.5 mm (2). The anterodorsal margins of the ears are separated by a small space in *Cynomops* and *Mormopterus*. In contrast, the anterodorsal ear pinnae are separated by a space of more than 4.5 mm in *Molossops*, and joined in a common point in *Eumops*. This character was previously used by Gregorin (2009: character 5) and Gregorin and Cirranello (2015: character 19).

Character 04: Shape of the ear pinna

Ears pinna triangular in shape (0), or rounded (1). *Cynomops*, *Molossops* and *Mormopterus* have triangular-like ears, while *Eumops* have blunt and rounded ears. This character was

previously used by Tavares (2008: character 44), Gregorin (2009: character 3) and Gregorin and Cirranello (2015: character 21).

Character 05: Anterodorsal surface of the ear pinna

Anterodorsal surface of the ear pinna smooth (0), or covered with warts (1). *Cynomops* and *Molossops* have smooth ears, while *Eumops* and *Mormopterus* have small warts surrounding the upper border of ears. This character was previously used by Gregorin (2009: character 6).

Character 06: Body size

Small-median (0) sized, or large (1). Most *Cynomops* species, *Molossops* and *Mormopterus* are small to median in size (Males: FA < 40mm, GLS < 20mm; Females: FA < 39 mm, GSL < 18mm). In contrast, *C. abrasus*, *C. mastivus* and *Eumops* are large (Males: FA > 42mm, GLS > 20mm; Females: FA > 40mm; GSL > 19mm). *Cynomops greenhalli* and *C. mexicanus* tend to be larger than the other small-median *Cynomops*, but there is overlap in the measurements. This character was previously used by Tavares (2008: character 42) and Gregorin (2009: character 10).

Character 07: Color of ventral pelage compared to the color of the dorsum

Ventral pelage coloration uniform along the ventral body axis, and overall similar or slightly paler than dorsum (0), or not uniformly paler than dorsum, mainly at the midventral region (1), or uniformly lighter than dorsum (2), or abdomen and gular region much paler than dorsum, usually whitish or pale-buff (3). The ventral pelage color is uniform, and similar or slightly paler than dorsum in *C. abrasus* and *C. mastivus*. A similar pattern is found in *C. greenhalli* and *C. milleri*, but the ventral pelage is not uniform and may include a lighter band. *Cynomops mexicanus* have uniform and lighter venter, while *C. planirostris* have the gular and midventral region much paler than dorsum, usually whitish or pale buff.

Upper and lower dentition

Character 08: Shape of upper incisors

Upper incisors conical (0), or flattened buco-lingual (1). The upper incisors are flattened buco-lingual in *Cynomops*, *Molossops* and *Eumops*. In contrast, *Mormopterus* has conical upper incisors. This character was previously used by Tavares (2008: character 166) and Gregorin (2009: character 15).

Character 09: Number of upper premolars

One upper premolar at each ramus (0), or two (1). *Cynomops*, *Molossops* and *Mormopterus* have one pair of upper premolars and *Eumops* has two pairs. This character was previously used by Gregorin (2009: character 17) and Gregorin and Cirranello (2015: character 54).

Character 10: Length of third premetacrista on M3

Premetacrista on M3 developed, longer than the postmetacrista (0), or less developed, half the length of the postmetacrista (1), or greatly reduced to absent (2). The premetacrista on M3 is greatly reduced or absent in *Cynomops* and *Eumops*. In contrast, *Molossops* presents a lesser developed premetacrista, reaching a half-length of the postmetacrista. A third condition is found in *Mormopterus* that have a very long commissure on M3, which is longer than the postmetacrista. This character was previously used by Gregorin (2009: character 19) and Gregorin and Cirranello (2015: character 65).

Character 11: Number of lower incisors

Two lower incisors present in each ramus of the mandible (0), or one lower incisor (1). *Cynomops*, *Mormopterus* and *Eumops* have two lower incisors. In contrast, *Molossops* has one lower incisor. This character was previously used by Tavares (2008: character 181) and Gregorin and Cirranello (2015: character 45).

Character 12: Relative size of the first lower premolar

First lower premolar (p4) two-thirds or more of the height of the lower second premolar, p5 (1), or a half or less of height of the lower second premolar (0). The first lower premolar, p4, is a half or less of height of the lower second premolar, p5, in *Mormopterus* and *C. mexicanus*. In contrast, the p4 is two-thirds or more of height of the p5 in *Eumops*, *Molossops* and all others *Cynomops* species (except for *C. planirostris* that shows both states for this character).This character was previously used by Tavares (2008: character 209).

Character 13: Median ridge on lingual face of second lower premolar

Median ridge on lingual face of second lower premolar p5 vestigial or absent, (0), or present (1). *Cynomops mexicanus*, *Eumops* and *Mormopterus* do not have a median ridge on the lingual face of the second lower premolar (p5). In contrast, a median ridge on lingual face of the second lower premolar is well developed in *Molossops* and in all other *Cynomops* species. This character was previously used by Tavares (2008: character 212).

Character 14: Trigonid on lower first molar

Trigonid deep and narrow on first lower molar (0), or shallow and wide (1). The trigonid is deep and narrow in *C. abrasus*, *Eumops*, *Molossops* and *Mormopterus* (Fig. 4B). In contrast, the trigonid is shallow and wide in all other *Cynomops* species (Fig. 4A). This character was previously used by Gregorin (2009: character 20).

Character 15: Entoconid on third lower molar

Entoconid present on third lower molar (0), or absent (1). The entoconid is present as a distinct cusp on the distal lingual part of the talonid in *Mormopterus*. In contrast, the entoconid is absent in *Cynomops*, *Molossops*, and *Eumops*. This character was previously used by Tavares (2008: character 240) and Gregorin and Cirranello (2015: character 69).

Character 16: Hypoconulid on the lower molars

Hypoconulid present on lower molars (0), or absent (1). The hypoconulid is present as a distinct cusp on the most distal part of the talonid in *Eumops*, *Molossop*s and *Mormopterus*. In contrast, the hypoconulid is absent in *Cynomops*. This character was previously used by Tavares (2008: character 242).

Skull

Character 17: Length of rostrum

Length of rostrum more than 40% of the greatest length of the skull (0), or rostrum short, less than 40% of the greatest length of the skull (1). *Cynomops* and *Molossops* have short rostra, which is less than 40% of the greatest length of the skull. In contrast, *Eumops* and *Mormopterus* have long rostra, covering more than 40% of the greatest length of the skull. This character was previously used by Gregorin (2009: character 21) and Gregorin and Cirranello (2015: character 70).

Character 18: Anterior border of hard palate

Anterior border of hard palate emarginated, with upper incisors clearly separated at the base due the separation of the left and right premaxillary bodies (0), or anterior border of hard palate not emarginated, with left and right premaxillary bodies fused to each other (1). The anterior border of the hard palate is emarginated, with upper incisors clearly separated at the base due the separation of the left and right premaxillary bodies in *Mormopterus*. Otherwise, the anterior border of hard palate is not emarginated due to the fusion of the left and right premaxillary bodies in *Cynomops*, *Eumops*, and *Molossops*. This character was previously used by Freeman (1981: character 65), Giannini and Simmons (2007: character 1), Gregorin and Cirranello (2015: character 80).

Character 19: Angle between the post-orbital constriction and rostrum

Post-orbital constriction forming a smoothly angle with the rostrum in the dorsal view of the skull (0), or post-orbital constriction forming a sharply defined angle with the rostrum (1). The post-orbital constriction forms a gently sloping angle with the rostrum in *Eumops*, *Mormopterus* and *C. mexicanus*. A post-orbital constriction forming a sharply defined angle with the rostrum is observed in the remaining *Cynomops* species.

Character 20: Nasal process of premaxilla

Nasal process of premaxilla well-developed, with the lateral margin of the external nares straight (0), or nasal process reduced with lateral margin of the external nares concave (1). The nasal process of premaxilla is well-developed with the lateral margin of the external nares straight in *C. mastivus* and *C. greenhalli* (Fig. 6A). In contrast, the nasal process is reduced with the lateral margin of the external nares reduced and concave (Fig. 6B). This character is well developed and more easily observed in males. This character was previously used by Giannini and Simmons (2007: character 2).

Character 21: Anterior face of lacrimal ridges

Anterior face of lacrimal ridges slopes to the forehead in lateral outline (0), or arising steeply but sloping smoothly proximal to the forehead (1), or steeply, forming an abrupt angle with the forehead (2). The anterior face of lacrimal ridges slopes to the foreahead in *Mormopterus* and *Molossops*. In contrast, the anterior face of lacrimal ridges arises steeply but slopes smoothly proximal to the forehead in *C. abrasus*, *C. planirostris* and *C. mexicanus* (Fig. 5C, D). The third condition, steeply, forming an abrupt angle with the forehead is found in *C. greenhalli*, *C. mastivus* and *C. milleri* (Fig. 5A, B).

Character 22: Pair of incisive foramina

One pair of incisive foramina absent (0), or present (1). *Cynomops* and *Molossops* have one pair of incisive foramina. *Eumops* have only one incisive foramen (Gregorin, 2009). This

character is not applicable for *Mormopterus*. This character was previously used by Gregorin (2009: character 34).

Character 23: Arrangement of incisive and accessory foramina

Accessory foramen separated from the incisive foramina by a large gap; the three foramina with relative positions as to form an isosceles triangle (1), or incisive foramina located closer to the accessory foramen, the three foramina with relative positions as to form an equilateral triangle (0). The accessory foramen is displaced and relatively far from the incisive foramina, resulting in an arrangement similar to an isosceles triangle if drawn a line uniting the three foramina in *C. abrasus*, *C. greenhalli*, *C. milleri* and *Molossops* (Fig. 3B). In contrast, the three foramina are positioned more close to each other, resulting in an arrangement similar to an equilateral triangle in *C. mastivus*, *C. mexicanus* and *C. planirostris* (Fig. 3A). This character is not applicable for *Eumops* and *Mormopterus*.

Character 24: Fossa on the squamosal bone

Fossa on the squamosal posterior to the squamosal ramus of the zygomatic arch imperceptible or shallow (0), or deep (1), or very deep (2). A fossa in the squamosal bone, located posterior to squamosal ramus of zygomatic is almost imperceptible or shallow in some *Cynomops* species (e.g. *C. abrasus* and *C. planirostris*), but it is deep in *C. greenhalli* and *C. milleri*, and well developed and very deep in *C. mexicanus*. This character was previously used by Velazco (2005: character 22) and Tavares (2008: character 156).

Character 25: Development of lacrimal ridges

Lacrimal ridges well developed, forming a groove enclosing infraorbital canal opening (1), or lacrimal ridges poorly developed or absent, and not forming a groove (0). The lacrimal ridges are well developed and form a groove enclosing the infraorbital canal opening in

Cynomops and *Molossops*. In contrast, the lacrimal ridges are poorly developed or absent, not forming a groove in *Eumops* and *Mormopterus*.

Character 26: Mastoid process

Mastoid process projects laterally (1), or does not project laterally (0). The mastoid process in *Cynomops* and *Molossops* is well developed and projects laterally. This character was previously used by Tavares (2008: character 128).

Character 27: Basisphenoid pits

Basisphenoid pits vestigial or absent (0), present (1). The basisphenoid pits are absent in some *Cynomops* species (e.g. *C. abrasus* and *C. milleri*). In contrast, basisphenoid pits are present in *C. mexicanus*, *C. planirostris*, *Eumops*, *Molossops* and *Mormopterus*. This character was previously used by Gregorin and Cirranello (2015: character 81).

Character 28: Depth of basisphenoid pits

Basisphenoid pits shallow (0), or deep (1), or very deep (2). The basisphenoid pits in *C. planirostris*, *C. mexicanus* and *Mormopterus* are shallow, in contrast, the basisphenoid pits are deep in *Molossops* and very deep in *Eumops*. This character was previously used by Freeman (1981: character 69), Gregorin (2009: character 27) and Gregorin and Cirranello (2015: character 83).

Character 29: Symphyseal region of the mandible

Well-developed "osseous" chin absent (0), or squared-shaped, well-developed osseous chin present (1). In *Cynomops* and *Molossops* there is no formation of a well-defined osseous chin, and the proximal portion of the mandibular ramus is gently curved. In contrast, a squared-shaped osseous chin is well-developed in *Mormopterus* and *Eumops*. This character was previously used by Tavares (2008: character 159).

Character 30: Development of mandible in males

Mandible massive with a convex corpus along its length in males (1), or gracile (0). Because *Cynomops* shows sexual dimorphism, some characters are more evident and/ or robust in males. One of these characters is the shape of the mandible, which tends to be more delicate in females, although there are the exceptions of the males of *C. abrasus*, which have gently curved mandibles along its length (Fig. 5D). All the remaining species of *Cynomops* have males with a massive mandible and a convex corpus along its length (Fig. 5B). This character was previously used by Gregorin (2009: character 35).

Character 31: Posterior mental foramen

Posterior mental foramen located at level between p4 and p5 (0), ventral to p5 (1), or ventral to space between the p5 and first molar (2). The posterior mental foramen is located ventral to space between the second premolar, p5, and first molar in *Cynomops*. In contrast, this foramen is ventral to second lower premolar, p5 in *Eumops* and *Molossops*. A third condition is observed in *Mormopterus* that presents the foramen between the p4 and p5. This character was previously used by Tavares (2008: character 164).

Postcranium morphology

Character 32: Relative development of the expanded costal cartilage of the first rib

Expanded costal cartilage of first rib relatively narrow, smaller than lateral process of manubrium (0), or well developed, its width roughly equals to that of the lateral process of the manubrium (1). The costal cartilage attached to the first rib is relatively narrow in some *Cynomops* species (e.g. *C. abrasus* and *C. planirostris*), while it is well developed in *Molossops*. I have not scored this character for *Eumops auripendulus*, *Mormopterus kalinowskii*, and *C. mexicanus* due to the lack of poscranium material and they were coded "?" in the data matrix. This character was previously used by Tavares (2008: character 275).

Character 33: Fossa between Crista pectoralis *and* Tuberculum majus *on the proximal end of the humerus*

Fossa between *crista pectoralis* and *tuberculum majus* small and rounded (0), or long and narrow (1), or long with a broader portion close to *crista pectoralis* (2). The fossa between *crista pectoralis* and *tuberculum majus* is small and rounded in *Molossops*. In contrast, it is long and narrow in *C. planirostris*. A third condition, long with a broader portion close to *crista pectoralis* is found in *C. abrasus*, *C. greenhalli*, *C. mastivus*, and *C. milleri*. I have not scored this character for *Eumops auripendulus*, *Mormopterus kalinowskii* and *C. mexicanus* due to the lack of poscranium material and they were coded "?" in the data matrix.

Penis

For penis morphology we scored *Mormopterus minutus* instead *M. kalinowskii* due to material availability, and we are therefore assuming that there is no variation of penis characters between these two taxa.

Character 34: Glans penis

Glans penis covered with spines (0), or spineless (1). *Cynomops* and *Molossops* have spines covering the glans penis (Figs. 2B, 3 B–D). In contrast *Mormopterus* and *Eumops* do not have spines on the glans penis (Supplementary information, Figs. 2A, 3A). I have not scored this character for *C. mexicanus* due to the lack of phalli material, and it was coded "?" in the data matrix. This character was previously used by Gregorin (2009: character 36).

Character 35: Ventral ridge of the glans penis

Ventral ridge of the glans penis covered with spines (0), or spineless (1). All *Cynomops* species, and also *Molossops* have a mid-ventral ridge on the glans penis (Supplementary

information , Figs. 3 B–D). This structure is spineless in *C. abrasus*, *C. greenhalli* (Fig. 3C), *C. mastivus*, and *C. milleri*, but is covered by spines in *C. planirostris* (Supplementary information, Fig. 3D). I have not scored this character for *C. mexicanus* due to the lack of phalli material, and it was coded "?" in the data matrix.

Character 36: Length of glans penis

Glans penis short, less than 2.00 mm in length (0), or long, more than 2.00 mm in length (1). The glans penis in *C. abrasus*, *C. mastivus* and *C. greenhalli* (Supplementary information, Fig. 3C) are longer (> 2.00 mm) than other *Cynomops* species, *Eumops*, *Molossops*, and *Mormopterus* (Supplementary information, Figs. 3 A, B and D). I have not scored this character for *C. mexicanus* due to the lack of phalli material, and it was coded "?" in the data matrix. This character was previously used by Gregorin (2009: character 38).

Character 37: Relative size of the ventral ridge of the glans penis

Ventral ridge is a half or more the size of the glans penis (0), or less than two-fifths the size of glans penis (1). The ventral ridge in *C. planirostris* and *Molossops* is well-developed occupying a half or more the size of the glans penis (Supplementary information, Figs. 3 B, D). In contrast, the others *Cynomops* species present a reduced ventral ridge, occupying less than two-fifths the size of the glans penis (Supplementary information, Fig. 3C). I have not scored this character for *C. mexicanus* due to the lack of phalli material, and it was coded "?" in the data matrix.

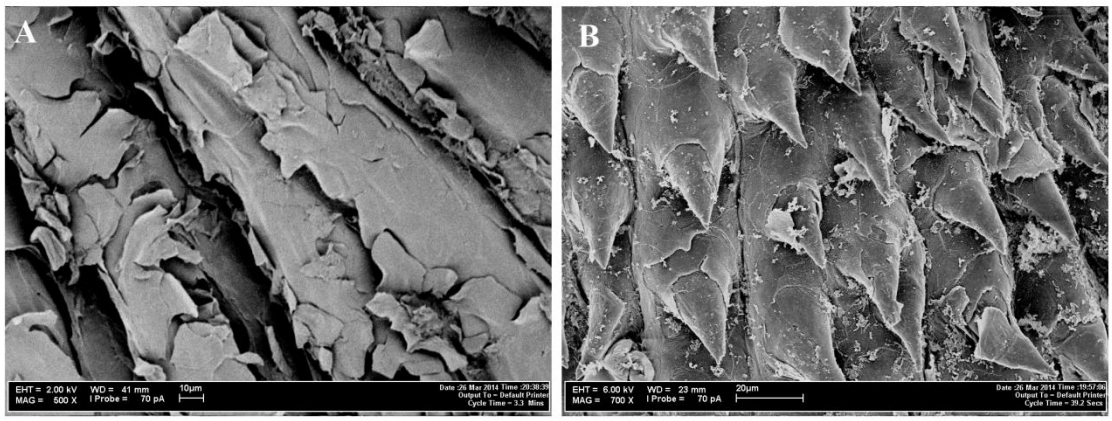
Character 38: Urinary meatus opening

Urinary meatus opens on the subterminal portion of the glans penis (0), or positioned on the terminal portion of the glans penis (1). The urinary meatus opens dorsal to the ventral ridge near its apex, exiting subterminally in *C. planirostris* and *Eumops* (Supplementary

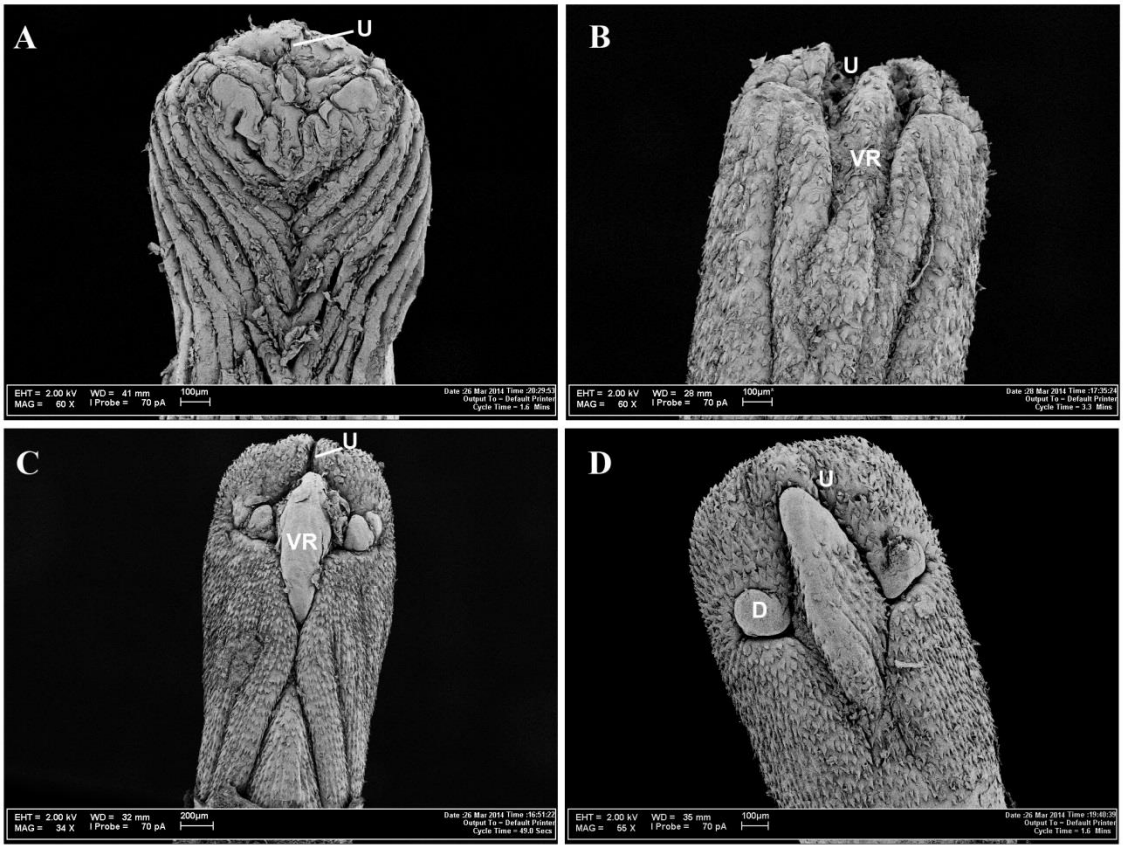
information, Fig. 3D). In contrast, the urinary meatus opens terminally in the other *Cynomops* species, *Mormopterus*, and *Molossops* (Supplementary information, Figs. 3 A–C). I have not scored this character for *C. mexicanus* due to the lack of phalli material, and it was coded "?" in the data matrix.

Character 39: Epithelial domes

Pair of epithelial domes absent on the ventral face of the glans penis (0), or pair of epithelial domes present (1). *Cynomops* have a pair of epithelial domes located lateral to the mid-ventral ridge on the ventral surface of the glans (Supplementary information, Figs. 3C, D). In contrast, *Eumops*, *Molossops*, and *Mormopterus* does not present the epithelium domes (Supplementary information, Figs. 3A, B). I have not scored this character for *C. mexicanus* due to the lack of phalli material, and it was coded "?" in the data matrix.



Supplementary information, Figure 2. Epithelial surface of the glans penis without spines in (A) *Mormopterus minutus* (USNM 311214), and covered by spines in (B) *Cynomops planirostris* (FMNH 20646).



Supplementary information, Figure 3. Ventral view of the distal glans penis in (A) *Mormopterus minutus* (USNM 311214), (B) *Molossops temminckii* (USNM 522947), (C) *Cynomops greenhalli* (USNM 339865), and (D) *C. planirostris* (FMNH 20646). U = urinary meatus, VR = ventral ridge; D = epithelial domes. Note the presence of a ventral ridge covered by spines in *M. temminckii* and *C. planirostris*, and spineless in *C. greenhalli*; the relative size of the ventral ridge, that is half or more the size of the glans penis in *M. temminckii* and *C. planirostris*, and less than two-fifths the size of glans penis in *C. greenhalli*; the terminal opening of the urinary meatus in *M. minutus*, *M. temminckii*, and *C. greenhalli*, and sub terminal in *C. planirostris*; and the presence of epithelial domes in both species of *Cynomops*.

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Revisionary Systematics of the small dog-faced bats (Molossidae: *Cynomops*) with the description of two new species

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Abstract

Bats from the genus *Cynomops* (Chiroptera: Molossidae) comprised seven species of fast flyers aerial insectivores distributed in the Neotropical region up to date. Our revisionary studies based on molecular, morphometric, and discrete morphological characters indicate the revalidation of *C. milleri* and suggested that *C. paranus* is junior synonym of *C. planirostris* and revealed two previously unrecognized, small forms of *Cynomops*. Here we provide an emended diagnosis and a redescription of *C. milleri*, and description of the two new species, *Cynomops* sp. 1 from Canal Zone region, Panama, sister to *C. mexicanus* and *Cynomops* sp. 2 from the eastern Andes of Ecuador and Colombia, sister to *C. milleri*.

Keywords: free-tailed bats; taxonomy; *Cynomops milleri*; *Cynomops* sp. 1; *Cynomops* sp. 2; Panama; eastern Ecuador.

1. Introduction

The dog-faced bats from the genus *Cynomops* Thomas, 1920 are fast-flyer, aerial insectivores that occur from Southern Mexico to Paraguay, and Northern Argentina, including Trinidad and Tobago (Goodwin and Greenhall, 1961; Koopman, 1982; Alvarez-Castañeda and Alvarez, 1991; Eger, 2008). *Cynomops* have been recorded in a variety of habitats, and are commonly found roosting abandoned houses (Bader *et al*., 2015). Differentiating among species of *Cynomops* is often difficult because of their external similarities, and diagnostic characters commonly used to distinguish among species of *Cynomops* have historically relied mainly in size variation and in patterns of pelage coloration (Simmons and Voss, 1998; Peters *et al*., 2002; Eger, 2008).

Except for the two large *Cynomops* (*C. abrasus* and *C. mastivus*), the other species of *Cynomops* have their size variation distributed in a continuum, and most of the measurements overlap (Peters *et al*., 2002). The lack of more precisely defined species delimitation boundaries within *Cynomops* have led to misidentifications and to several disputes regarding the status of some taxa (Koopman, 1993, 1994; Simmons and Voss, 1998; Peters *et al*., 2002; Eger, 2008). Among the small dog-faced bats, *Cynomops milleri* has one of the most controversial taxonomic histories. *Cynomops milleri* was described as pertaining to *Molossops* (Osgood, 1914), subsequently treated as a subspecies of *Cynomops planirostris* (Koopman, 1978, 1993, 1994) then synonymized with *C. paranus* (Simmons and Voss, 1998), and finally considered a separate species again (Eger, 2008). On the other hand, *C. paranus* was either described (Thomas, 1901) and treated as a subspecies of *C. planirostris* (Koopman 1978, 1993, 1994) or as a separate species (Handley, 1976; Simmons and Voss, 1998; Peters *et al*., 2002).

In spite of difficulties in determining the diversity contained in *Cynomops* more species have recently been described, and the genus is now composed by at least seven species endemic to the Neotropics including *Cynomops abrasus* (Temminck, 1827), *Cynomops greenhalli* Goodwin, 1958, *C. mastivus* (Thomas, 1911), *Cynomops mexicanus* (Jones and Genoways, 1967), *Cynomops milleri* (Osgood, 1914), *Cynomops paranus* (Thomas, 1901), and *Cynomops planirostris* (Peters, 1865) (Simmons and Voss, 1998; Peters *et al*., 2002; Moras *et al*., ms).

Recent phylogenetic analyses of molecular and morphological data recovered paraphyletic arrangements for *C. paranus* and *C. milleri*, and uncovered two previously unknown forms (Moras *et al*., ms). Data of Moras *et al*. (ms) and our ongoing revisionary studies of the small sized *Cynomops* revealed evidences that specimens formerly identified as *C. paranus* actually represent three species, one corresponding to *C. milleri*, and two previously undescribed forms. Herein, we present a comprehensive revisionary work of the small forms of *Cynomops*, summarizing the evidences to the recognition of *C. milleri* as a separate species and redescribing it, and provide the descriptions of two new species of small dog-faced bats.

2. Material and methods

2.1. Taxon sampling

Specimens examined for this study (see Appendix I) are deposited in the following collections:

AMNH American Museum of Natural History, New York, USA.

KU Biodiversity Institute, University of Kansas, Lawrence, USA.

INPA Instituto Nacional de Pesquisas na Amazônia, Manaus, Brazil.

FMNH	The Field Museum, Chicago, USA.
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.
ZMB	Museum für Naturkunde Berlin, Humboldt Universität, Berlin, Germany.
BMNH	Natural History Museum, London, UK.
ROM	Royal Ontario Museum, Toronto, Canada.
TTU/TK	Museum of Texas Tech University, Lubbock, Texas, USA.
QCAZ	Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
STRI	Smithsonian Tropical Research Institute, Balboa, Panama.
USNM	United States National Museum of Natural History, Washington DC, USA.

The nomenclature used to describe skull characters follows Freeman (1981) and Giannini *et al*. (2006). External and cranio dental characters are based on those defined by Velazco (2005), Giannini and Simmons (2007a), Tavares (2008), Tavares *et al*. (2014), Gregorin (2009), Gregorin and Cirranello (2015) and Moras *et al*. (ms). Our morphometric analyses were based on adults, with the exception of the type of *C. milleri* and a subadult individual (QCAZ 11791) with *synchondrosis sphenoccipitalis*, and the epiphyses not completely fused. Juvenile specimens were included on our observations for discrete characters based on specimen availability. For tooth nomenclature, we follow Giannini and Simmons (2007b) assuming that the second lower premolar is lost in Chiroptera, and Gregorin and Cirranello (2015) considering the premolar arrangement of p1, p4 and p5 for molossids.

We recorded external and craniodental measurements in millimeters (mm) using digital calipers accurate to 0.01 mm; body mass is in grams (g). Measurements are defined as follows:

Forearm length (FA), distance from the tip of the olecranon process to wrist (including carpals), and taken with the wing partially folded.

Greatest length of the skull (GLS), distance from the posteriormost point at the occipital bone to the anteriormost point on premaxillar bone.

Braincase breadth (BB), greatest breadth of braincase.

Mastoid breadth (MB), greatest breadth across mastoid region.

Rostral width (ROS), greatest breadth across the lacrimal ridges.

Condyloincisive length (CIL), distance from the posteriormost margins of occipital condyles to the anterior face of upper incisor(s).

Zygomatic breadth (ZB), greatest breadth across zygomatic arches

Postorbital breath (POB), least breadth measured in the postorbital region, always posterior to the postorbital process when present.

Maxillary toothrow length (MTRL), distance from the anterior face of the upper canine to the most posterior edge of the last upper molar.

Breadth across upper molars (BM), least breadth across the last upper molars.

Width across upper canines (C-C), least width across the upper canines.

Mandible length (ML), from the mandibular symphysis to the condyloid process.

2.2. Morphometric analysis

We performed Student´s t-tests ($p \leq 0.05$) for the variation between sexes of the putative species. We also employed multivariate analyses (Principal Component, PCA and Discriminant Function analyses DFA), and MANOVA tests, to visualize and test the variation across all species. All multivariate analyses were carried out using 12 $\log_{10}$-transformed measurements (FA, GLS, POB, ROS, C-C, ZB, BB, MB, MTRL, BM, CIL,

and ML) of five currently known species of *Cynomops* and the two hypothetical new forms. Missing data up to three measurements by specimen were estimated using the expectation-maximization method, as described by Dempster *et al*. (1977). Statistical analyses were performed using Past v. 2.17 (Oslo, Norway) (Hammer *et al*., 2001), Systat version 11.0 and Minitab® (State College, PA, USA).

3. Results

We examined 242 adult specimens of *Cynomops* (79 males and 163 females), including all holotypes, and representing seven species (see Appendix). We detected sexual dimorphism for all measurements ($p < 0.01$) for all forms, and therefore males and females were treated separately in all analyses.

Most of the variation was explained by the two first components in the PCA (Figs. 1A, B). For males, the plot of these components displayed a clear separation in size between the smallest (*C. planirostris* and *Cynomops* sp. 2) and the medium-sized *Cynomops* (*C. greenhalli*, *C. mexicanus*, and *Cynomops* sp. 1). The specimens *a priori* identified as *C. paranus* including the holotype (BMNH 1.7.11.15 ♂) overlapped with both, the smaller and the medium-sized clusters of specimens *Cynomops* (Fig. 1A). Similar patterns were observed for females (Fig. 1B), with the two individuals of *C. milleri*, the type (FMNH 19652), and the individual from Venezuela similar in size with *C. planirostris* (Fig. 1B).

Most measurements varied equally and positively with size for males along PC 1, but the post-orbital breadth (POB), rostral width (ROS), zygomatic breadth (ZB) and mastoid breadth (MB) were not proportional to the characters related to skull length (e.g., GLS), braincase breadth (BB) and teeth breadth (C-C and BM) as demonstrated by the

variation along PC2 (Table 1). The eigenvector values also varied positively along the PC 1 for females, but the measurements related to skull length (e.g. GLS, MTRL) were not proportional to characters associated to skull breadth as demonstrated by the negative values in PC 2 (Table 2).

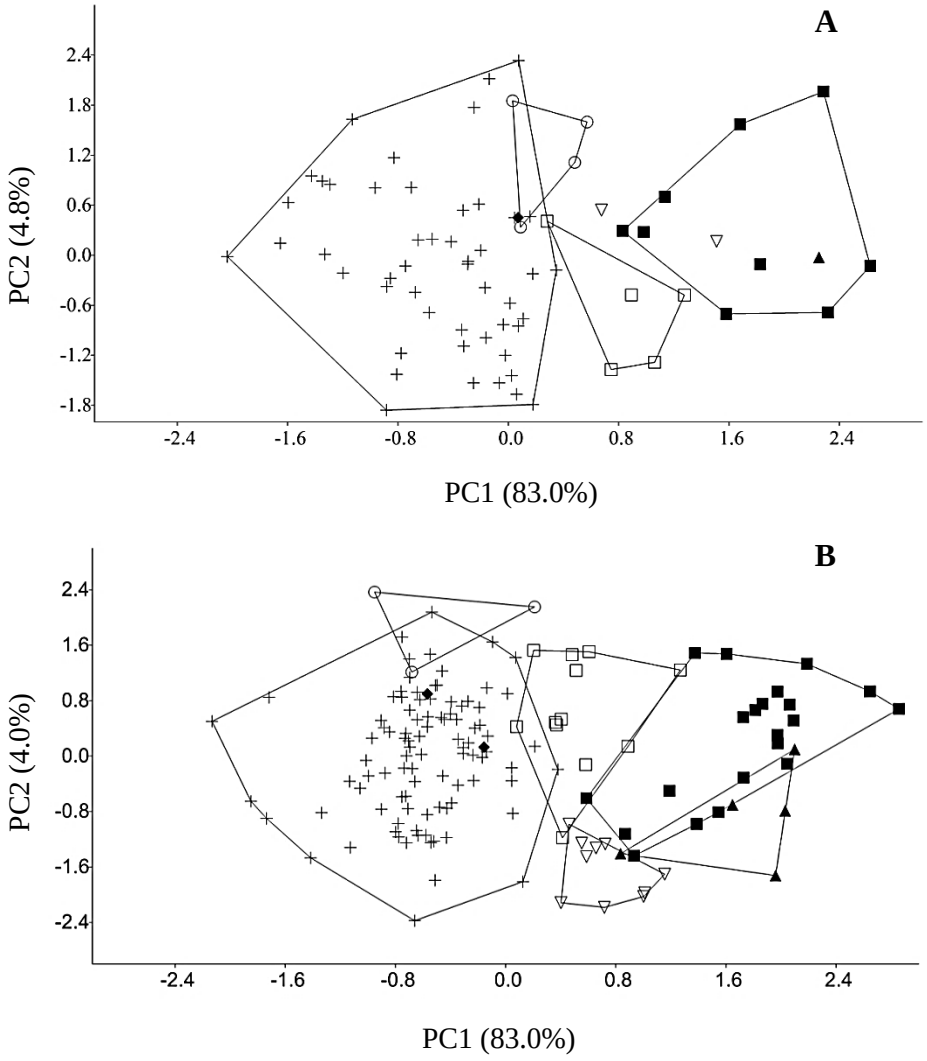

Figure 1. Plot of the first and second principal component scores of a PCA analysis based on 12 cranial, mandibular, and external measurements for (A) males and (B) females of *C. planirostris* (cross), *Cynomops* sp. 2 (circles); *C. paranus* (empty squares); type of *C. paranus* (full diamond); *C. mexicanus* (triangles); *C. greenhalli* (full squares); *Cynomops* sp. 1 (invert triangles) and *C. milleri* (full diamonds).

Table 2. Vector correlation coefficients (loadings) between original variables and principal components (PC1 and PC2) and between original variables and discriminant functions (DF1 and DF2) for analyses including representatives of all males of small sized *Cynomops*, and excluding *C. planirostris* and species represented by only one individual (Reduced). Values in boldface indicate vector correlations with magnitudes > 0.30.

	Loadings of PCA and DFA							
	All species				Reduced			
Characters	PC1	PC2	DF1	DF2	PC1	PC2	DF1	DF2
GLS	0.29	0.10	**0.57**	0.10	0.27	0.04	**1.43**	**0.94**
POB	0.26	-0.12	-0.10	-0.27	0.27	-0.03	**0.43**	**-1.46**
ROS	**0.33**	-0.28	**-0.87**	**-0.41**	**0.37**	-0.15	**-2.48**	**0.43**
C-C	**0.31**	0.28	0.16	**-0.47**	0.22	0.29	**-0.74**	**0.66**
ZB	**0.32**	-0.17	**0.49**	**0.61**	**0.39**	-0.19	**2.67**	-0.25
BB	0.27	0.04	0.14	**-0.84**	0.26	**0.31**	-0.09	0.28
MB	**0.32**	**-0.69**	0.29	**0.86**	**0.32**	**-0.71**	**0.58**	**-0.58**
MTRL	0.26	**0.35**	0.25	**1.31**	0.25	0.21	**0.91**	**1.08**
BM	0.27	0.16	**0.43**	-0.20	0.24	-0.05	**0.95**	-0.28
CIL	0.29	0.06	0.20	-0.08	0.26	0.12	**-2.44**	**-1.46**
ML	**0.30**	0.08	**-0.57**	**-0.40**	0.29	0.10	**-0.50**	**0.79**
FA	0.24	**0.40**	0.12	-0.28	0.26	**0.42**	**1.06**	-0.11

Table 3. Vector correlation coefficients (loadings) between original variables and principal components (PC1 and PC2) and between original variables and discriminant functions (DF1 and DF2) for analyses including representatives of all females of small sized *Cynomops*, and excluding *C. planirostris* (Reduced). Values in boldface indicate vector correlations with magnitudes > 0.30.

	Loadings of PCA and DFA							
	All species				Reduced			
Characters	PC1	PC2	DF1	DF2	PC1	PC2	DF1	DF2
GLS	0.29	-0.04	0.19	**0.43**	0.27	-0.07	0.04	0.08
POB	0.25	**0.63**	-0.21	**0.60**	0.22	**0.61**	**0.56**	**-0.64**
ROS	**0.30**	0.09	-0.18	0.10	**0.35**	0.13	-0.07	**-0.70**
C-C	**0.35**	**-0.41**	**0.52**	0.04	0.27	**-0.33**	-0.18	0.25
ZB	**0.31**	0.06	**0.31**	**0.41**	0.29	0.05	-0.28	**-0.92**
BB	0.24	**0.52**	0.05	**0.30**	0.20	**0.51**	**0.66**	0.12
MB	**0.30**	0.04	0.27	**-0.29**	**0.30**	-0.09	**-0.58**	-0.08
MTRL	0.28	**-0.30**	-0.27	**-1.09**	**0.35**	**-0.36**	**-0.71**	**0.80**
BM	0.29	-0.19	0.10	0.19	0.26	-0.09	0.00	0.12
CIL	0.27	-0.09	0.29	**-0.49**	0.27	-0.17	**084**	**0.90**
ML	**0.30**	-0.11	0.05	-0.10	**0.32**	-0.09	**-0.96**	**-0.40**
FA	0.24	0.06	0.12	0.11	**0.31**	0.21	**-0.30**	**-0.32**

The first two discriminant functions accounted for the most of the among-group variation (Figs. 2A, B). For males, the scores of *C. mexicanus*, *Cynomops* sp. 1, and the group formed by *Cynomops* sp. 2 did not overlap with those of the other species (Fig. 2A). In contrast, the clusters containing *C. planirostris*, *C. paranus*, and *C. greenhalli* overlap. All female clusters overlap, with the exception of that formed by *Cynomops* sp. 2 (Fig. 2B). The adult female *C. milleri* from Venezuela nested within the *C. paranus* grouping (Fig. 2B).

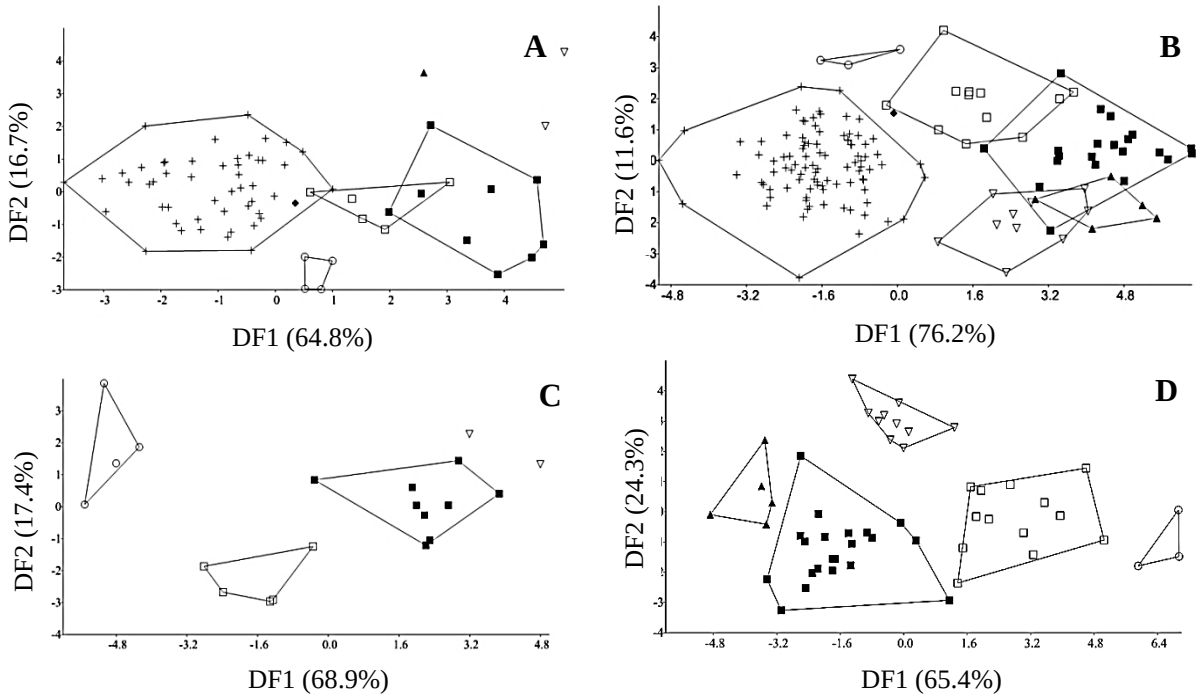

Figure 2. Plots of scores of the first and second discriminant functions including representatives of all male groups of small sized *Cynomops* (A) and females (B). Plots of scores of the first and second discriminant functions excluding *Cynomops planirostris* and the unique individual of *C. mexicanus* for males (C) and females (D). *C. planirostris* (cross); *Cynomops* sp. 2 (circles); *C. paranus* (empty squares); type of *C. paranus* (full diamond); *C. mexicanus* (triangles); *C. greenhalli* (full squares); *Cynomops* sp. 1 (invert triangles) and *C. milleri* (full diamonds).

After removing the single male individual of *C. mexicanus*, and all individuals of *C. planirostris* the clusters of *C. paranus*, *C. greenhalli*, *Cynomops* sp. 1, *Cynomops* sp. 2, and *C. mexicanus* were clearly separated (Males: Wilk's lambda=0.001, df= 48, 21, p = 0.008; Females: Wilk's lambda= 0.01, df= 60, 167, p = < 0.0001) (Figs. 2C, D). From the twelve metric characters analyzed, eleven were useful to distinguish between species for males, and nine were useful in the case of females (Tables 1 and 2). All morphometric characters can be used in combination for the distinction between species (Table 3).

We could not differentiate the types of *C. planirostris* and *C. paranus* based on our revisionary studies, based on both molecular and morphological evidences, suggesting that *C. paranus* should be synonymized with *C. planirostris*. The darker dorsal and ventral pelage coloration observed by Thomas (1901) and by Simmons and Voss (1998) is also present in series from Brazilian Amazonia, states of Pará and Amazonas (AMNH 79731 and 79733, 92253–55, 92971, 93879– 93887, 94630–94653), and may be explained by geographical or individual variation.

On the other hand, the individuals called "*C. paranus*" from Guiana Shield and Brazilian Amazon correspond to the descriptions and characters of the type of *C. milleri* including the shape of braincase "(…) braincase broad and bulging laterally (…)" (Osgood, 1914: 183). *Cynomops milleri* and "*C. paranus*" also formed a clade supported by molecular and morphological data (Moras *et al*. ms). According to our observations, the smaller size commonly used to distinguish *C. milleri* from the other *Cynomops* species is not a useful diagnostic character for this taxon (see table 3). The recognition of *C. milleri* deserves a redescription and an emended diagnosis:

Systematics

Family Molossidae Gervais 1856

Genus *Cynomops* Thomas 1920

Cynomops milleri (Osgood, 1914)

Miller's Dog-faced Bat

Figures 4–6

Molossops milleri Osgood, 1914b:183; type locality "Yurimaguas," Loreto, Peru.

Cynomops milleri: Thomas, 1920:189; first use of the current name combination.

Molossops (*Cynomops*) *milleri*: Cabrera, 1958:119; name combination.

Molossops planirostris milleri: Koopman, 1978: 20; name combination; not Peters, 1865

Molossops paranus: Handley, 1976: 39; part, not Thomas, 1901

Molossops (*Cynomops*) *paranus*: Simmons and Voss, 1998: 149; part, not Thomas, 1901

Cynomops paranus: Peters *et al*. (2002): 1100; part, not Thomas, 1901

TYPE MATERIAL: The holotype FMNH 19562 is relatively well-preserved skin and skull of a subadult female from Yurimaguas, Department of Loreto, Peru, collected by M. P. Anderson (no. 61) on September 30, 1912, during the Anderson-Osgood Expedition to northern Peru.

MEASUREMENTS OF THE HOLOTYPE: FA 30.3, GLS 15.49, POB 4.42, ROS 6.52, C-C 4.32, ZB 10.52, BB 8.30, MB 9.82, MTRL 5.91, BM 7.38, CIL 15.2, ML 11.21. Additional measurements (mm) are from Osgood (1914): Total length 83, tail 26, foot 6.5, lower leg 10, third digit, metacarpal 29.7, first phalanx 13.2, second phalanx 11, breadth of anterior nares 2.7.

DISTRIBUTION: *Cynomops milleri* is known from the lowlands (26–242 m a.s.l.) of northern and eastern South America, from the eastern slopes of the Andes in Venezuela, Guyana, Surinam, French Guiana, northern Peru, and from the western Brazilian Amazonia (Fig. 3).

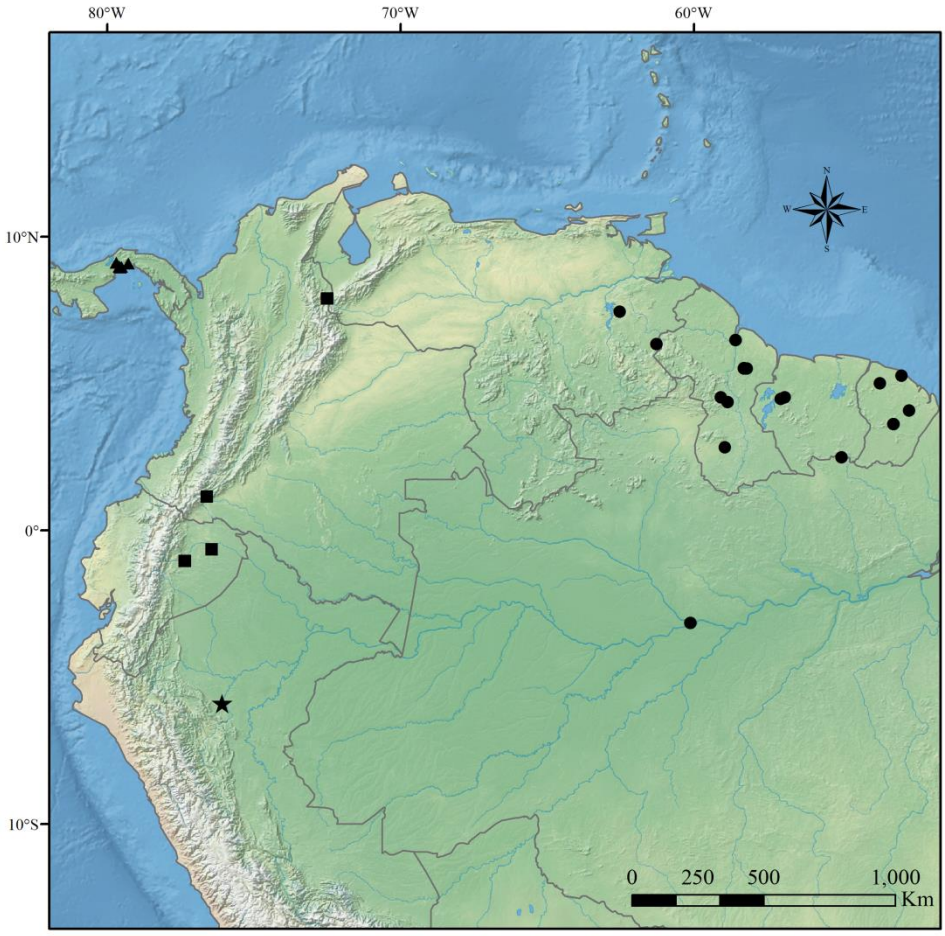

Figure 3. Map showing collecting localities of *Cynomops sp. 1*, sp. nov. (triangles), *Cynomops sp. 2*, sp. nov. (squares), and *C. milleri* (circles; type locality represented by star).

EMENDED DIAGNOSIS: A small *Cynomop*s (males: FA 34.00–37.00, n=6; GLS 16.71–18.23, n=6; females: FA 30.30–35.00 n=6; GLS 15.49–16.50 n=14; Table 3). Dorsal pelage varies from dark-chocolate-brown to lighter reddish-brown; the ventral coloration is slightly paler than dorsum, with variable presence of a conspicuous whitish portion from gular to the

mid-ventral region; the rostrum is short and broad; the anterior face of the lacrimal ridge form an abrupt angle with the forehead (Figs. 4A, D; 5A, D); the nasal process of the premaxilla is reduced, with the lateral margin of the external nare concave; the incisive foramina are located much posterior to the accessory foramen, the arrangement of the three foramina (incisive and accessory) form an isosceles triangle (Fig. 6B); the basisphenoid pits are absent; a shallow fossa is present in the posterior squamosal bone, where the zygoma meets the braincase; a well-developed median ridge is present in the lingual face of the second lower premolar (p5); the first lower premolar (p4) is approximately two-thirds or more of the height of the second lower premolar.

Cynomops milleri here including part of the individuals formerly identified as *C. paranus*, is sister group of *Cynomops sp. 2*, sp. nov. and both are sister group of the large *Cynomops*, *C. abrasus*, *C. mastivus* and *C. greenhalli* (Moras *et al*. ms).

REDESCRIPTION: *Cynomops milleri* is externally similar to *C. greenhalli* but slightly smaller in size (Table 3). The dorsal pelage coloration varies from dark-chocolate-brown to light reddish-brown, and the ventral pelage is pale, and more conspicuously whitish in a portion of the venter departing from the gular to the mid-ventral region. Pelage is silky, but the dorsal fur is not very long (4 mm in length, taken on the level of the scapular area); the individual dorsal hairs are bicolored, with the basal half of each hair pale-buff.

The face is blackish and virtually naked; the upper lip and the dorsal border of the narial region are smooth; the triangular and blackish ears are slightly separated one from the other at the forehead (space ≤ 4.0 mm); the patagium, feet and tail are also blackish; the propatagium is narrow, and the posterior plagiopatagium is inserted lateral to the base of the foot. There is dark-chocolate-brown or reddish-brown fur distributed along one-third of

the forearm, and to the adjacent propatagium. A second patch of fur extends from the posterodorsal surface of distal plagiopatagium next to the wrist, to dactilopatagium IV.

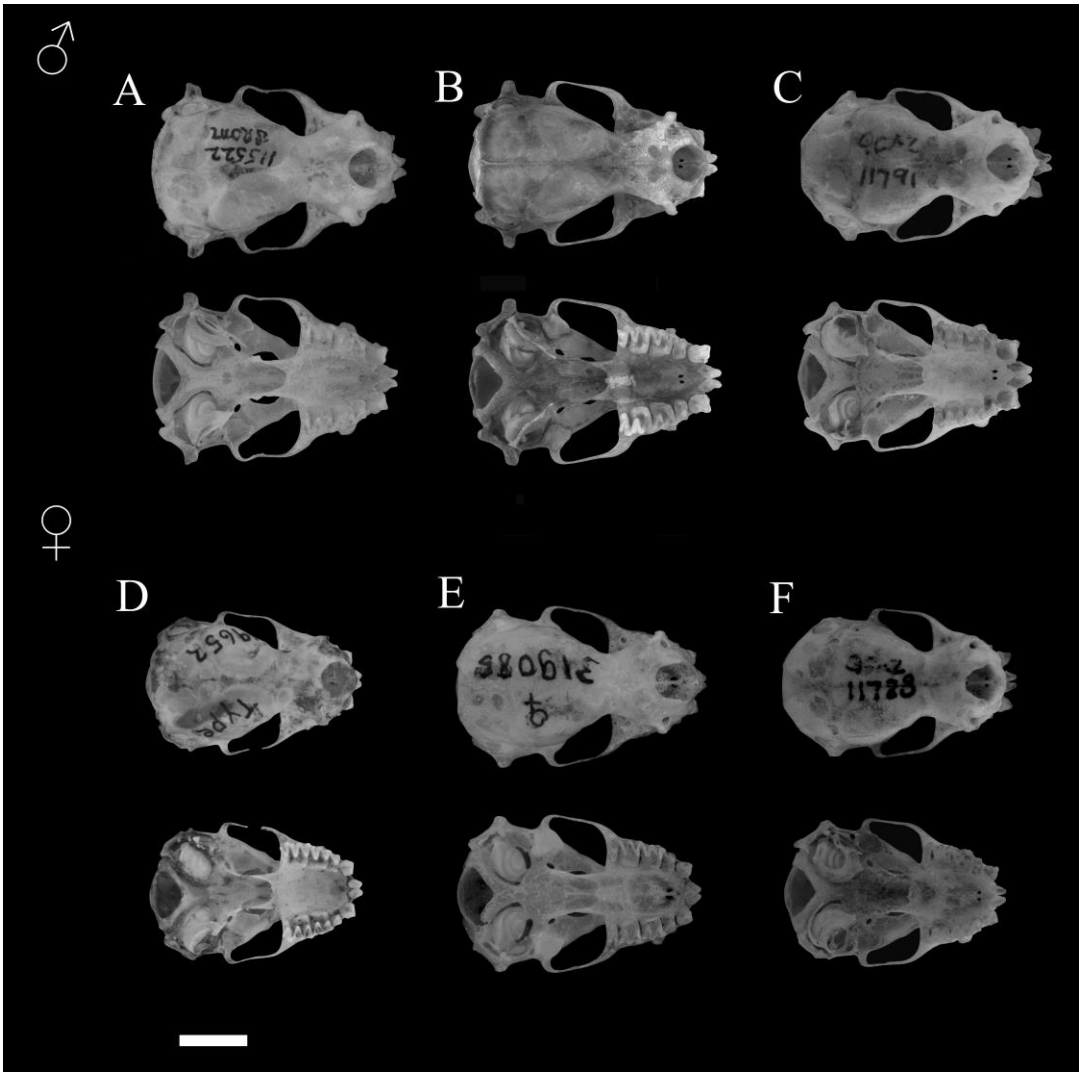

Figure 4. Dorsal and ventral view of males of (A) *C. milleri*, (B) *Cynomops* sp. 1, STRI 80 [holotype], and (C) *Cynomops* sp. 2. Dorsal and ventral view of females of (D) *C. milleri* FMNH 19652 [holotype], (E) *Cynomops* sp. 1, and (F) *Cynomops* sp. 2, QCAZ 11788 [holotype]. Scale bar = 5 mm.

The skull is rounded, with a broad and bulging laterally braincase; the post-orbital constriction forms a sharply defined angle with the rostrum; the sagittal and occipital crests

are consistently well developed in males; the anterior face of lacrimal ridges forms an abrupt angle with the forehead (Figs. 4A, D; 5A, D); the nasal process of the premaxilla is reduced, with the lateral margin of the external nares concave; the incisive foramina are located relatively farther to the accessory foramen (Fig. 6B). Basisphenoid pits are absent, and there is a shallow fossa on the posterior squamosal bone, where the zygoma meets the braincase (Velazco, 2005: 12). The mandible is massive in males, and has a concave corpus along its length (Fig. 5A). There is a well-developed median ridge on the lingual face of the second lower premolar, and the first lower premolar is two-thirds or more of the height of the second lower premolar.

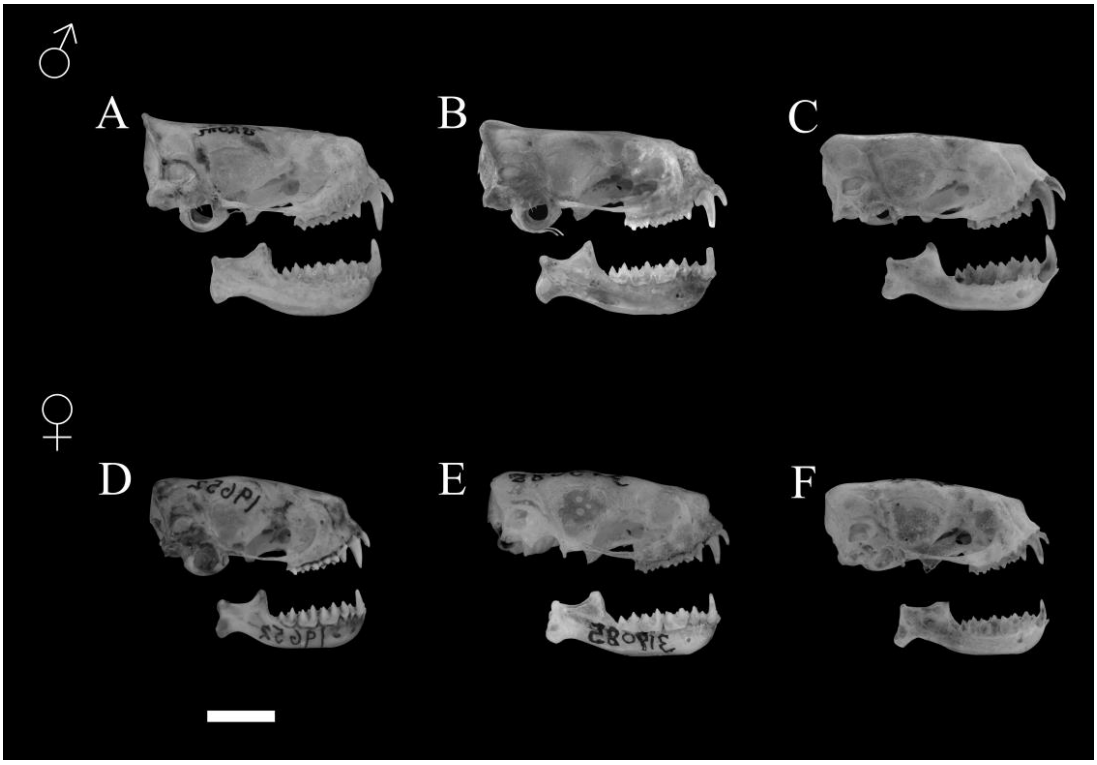

Figure 5. Lateral view of males of (A) *C. milleri*, (B) *Cynomops* sp. 1, STRI 80 [holotype], and (C) *Cynomops* sp. 2. Lateral views of females of (D) *C. milleri* FMNH 19652 [holotype], (E) *Cynomops* sp. 1, and (F) *Cynomops* sp. 2, QCAZ 11788 [holotype]. Scale bar = 5 mm.

Table 4. Measurements (mm) of adults of small-median sized *Cynomops.* See Material and Methods for variable abbreviations. Statistics include the mean, range (in parentheses) and sample size.

	C. greenhalli		*C. mexicanus*		*Cynomops* sp. 1	
Number/ sex	9 males	22 females	1 male	5 females	2 males	10 females
Weight	18.97 (16–23.9) 3	16.48 (10.80–19.10) 5	–	13.5 (11, 16) 2	19.00	17.15 (13.00–19.00) 6
FA	37.41 (35–39.7) 11	35.36 (33.40–38.28) 22	37.05	35.08 (33.02–36.3) 5	36.00, 36.10	33.00 (32.64–33.50) 10
GLS	18.41 (17.37–19.23) 9	17.12 (15.91–17.82) 21	18.78	17.02 (15.87–17.57) 5	17.65, 18.37	16.58 (16.37–17.00) 9
POB	4.78 (4.53–5.02) 9	4.63 (4.29–4.97) 21	4.73	4.53 (4.23–4.80) 5	4.35, 4.52	4.29 (4.19–4.36) 10
ROS	8.28 (7.63–9.13) 9	7.37 (6.99–7.91) 20	8.53	7.10 (6.87–7.27) 5	6.70, 7.89	6.88 (6.59–7.19) 10
C-C	5.45 (5.16–5.71) 9	4.80 (4.64–5.05) 20	5.81	4.84 (4.74–5.07) 5	4.52, 5.42	4.68 (4.51–4.94) 10
ZB	12.77 (12.06–13.65) 9	11.85 (11.23–12.51) 16	13.20	11.76 (11.32–12.00) 5	10.72, 12.68	11.13 (10.81–11.36) 8
BB	9.24 (8.68–9.65) 9	8.86 (8.20–9.25) 20	9.18	8.75 (8.65–8.92) 5	7.91, 8.71	8.28 (8.09–8.50) 9
MB	12.26 (11.9–13.01) 7	11.24 (10.49–11.86) 17	13.16	11.21 (10.71–11.41) 4	11.00, 12.81	10.82 (10.51–11.16) 9
MTRL	7.18 (6.79–7.67) 9	6.61 (6.22–7.05) 21	7.62	6.79 (6.38–6.92) 5	6.38, 7.47	6.45 (6.33–6.68) 10
BM	8.39 (8.02–8.84) 9	7.96 (7.44–8.53) 21	8.45	8.12 (7.71–8.48) 5	7.46, 8.42	7.72 (7.38–8.03) 10
CIL	18.68 (17.92–19.5) 9	16.93 (16.06–17.68) 21	19.39	16.87 (16.05–17.19) 5	16.13, 18.91	16.50 (16.26–16.94) 7
ML	13.66 (13.08–14.25) 9	12.55 (11.80–13.14)	14.31	12.81 (12.58–13.02)	12.11, 13.51	11.95 (11.75–12.18) 10

	C. planirostris		*C. milleri*		*Cynomops* sp. 2	
	57 males	106 females	6 males	17 females	4 males	3 females
Weight	12.63 (10.00–15.00) 10	10.86 (8.60–14.00) 15	18.52 (16.20–20.00) 6	14.29 (12.00–16.00) 7	14.65 (14.00, 15.30) 2	13.5 (12.8–14.8) 3
FA	33.57 (31.36–36.56) 50	32.20 (29.00–34.92) 83	35.17 (34.00–37) 6	33.02 (30.30–35.00) 15	34.89 (34.38–35.45) 4	31.81 (31.28–32.57) 3
GLS	16.33 (15.21–17.29) 46	15.40 (14.11–16.20) 93	17.48 (16.71–18.23) 6	16.09 (15.49–16.51) 14	17.28 (17.12–17.53) 4	15.62 (15.13–16.05) 3
POB	4.33 (3.92–4.90) 48	4.22 (3.80–4.56) 96	4.74 (4.64–4.83) 6	4.47 (4.36–4.72) 17	4.44 (4.27–4.69) 4	4.44 (4.31–4.68) 3
ROS	7.32 (6.49–7.95) 49	6.57 (5.94–7.08) 96	7.85 (7.19–8.24) 6	6.76 (6.43–7.22) 16	7.63 (7.44–7.74) 3	6.59 (6.25–6.97) 3
C-C	4.85 (4.34–5.25) 49	4.23 (3.88–5.07) 97	5.20 (5.04–5.45) 6	4.51 (4.32–4.81) 17	5.26 (4.96–5.44) 4	4.27 (4.06–4.46) 3
ZB	11.19 (9.88–12.00) 46	10.52 (9.54–11.19) 80	11.97 (11.49–12.42) 6	11.02 (10.52–11.64) 12	11.55 (11.40–11.80) 3	10.68 (10.41–10.91) 3
BB	8.21 (7.63–8.84) 47	8.07 (7.54–8.51) 94	8.75 (8.53–9.09) 6	8.55 (8.28–8.90) 17	8.71 (8.67–8.74) 4	8.42 (8.28–8.55) 3
MB	11.03 (9.68–11.91) 40	10.06 (9.27–10.98) 89	12.10 (11.39–12.46) 5	10.45 (9.76–11.29) 14	11.02 (10.79–11.21) 4	10.16 (10.02–10.25) 3
MTRL	6.45 (5.91–6.97) 49	6.02 (5.52–6.63) 97	6.76 (6.61–6.87) 6	6.08 (5.38–6.29) 16	6.69 (6.54–6.83) 4	5.73 (5.59–5.96) 3
BM	7.49 (7.02–8.10) 49	7.21 (6.34–7.68) 97	8.11 (7.84–8.46) 6	7.62 (7.15–7.89) 16	7.85 (7.68–8.02) 4	7.13 (6.90–7.38) 3
CIL	16.65 (15.29–17.52) 45	15.33 (14.34–16.39) 87	17.70 (17.26–18.51) 6	15.91 (15.20–16.56) 15	17.64 (17.39–17.95) 3	15.41 (15.09–15.79) 3
ML	12.13 (11.12–12.83) 48	11.27 (10.20–12.19) 97	12.80 (12.40–13.43) 6	11.63 (11.16–12.04) 17	12.62 (12.43–13.05) 4	11.17 (11.00–11.38) 3

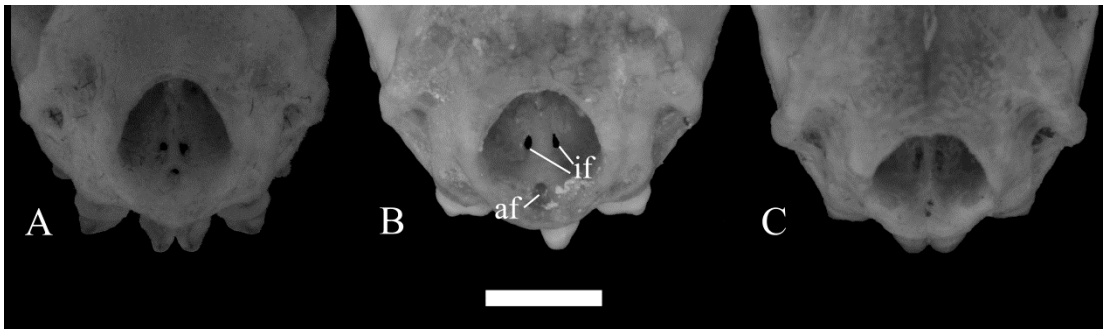

Figure 6. Configuration of the incisive foramina and accessory foramen in (A) *Cynomops* sp. 2 (QCAZ 11789; female), (B) *C. milleri* (AMNH 79745, female), and (C) *Cynomops* sp. 1 (AMNH 183865, female). Note that the accessory foramina is located relatively closest from the incisive foramina in *Cynomops* sp. 2, and farther in *C. milleri and Cynomops* sp. 1. Scale bar = 5 mm.

COMPARISONS: *Cynomops milleri* resembles *C. greenhalli* more closely, and both can be distinguished from the other two small species of *Cynomops* (*C. mexicanus* and *C. planirostris*) by the patterns of ventral pelage coloration. The venter is slightly paler than the dorsum, but general ventral pelage is more whitish in the region that passes from the gular to the mid-ventral region in *C. milleri* and *C. greenhalli*, but is much paler than dorsum in *C. mexicanus* that also has a bright white venter all along the mid-ventral region. *Cynomops milleri* and *C. greenhalli* can also be separated from the other small-median species by the abrupt angle formed by the rostrum and the forehead, which slopes smoothly proximal to the forehead in *C. mexicanus* and *C. planirostris*.

Cynomops milleri can be distinguished from *C. greenhalli* by its relatively small size (Table 3); relatively short rostrum (MTRL Males: 6.61–6.87 mm; females: 5.38–6.29 mm), which is longer in *C. greenhalli* (MTRL Males: 6.79–7.67 mm; females: 6.22–7.05 mm); by the basal half of each dorsal hair colored pale-buff, while the hair of *C. greenhalli* has a basal third of each individual dorsal hair pale colored; and by the reduced nasal process of the premaxilla, which is well developed in *C. greenhalli*. Genetic distances for

the Cytochrome *b* mitochondrial region varied from 4.6 to 12.3% comparing *C. milleri* to other *Cynomops* species (Moras *et al*. ms).

REMARKS: A young individual of *C. planirostris* with skull sutures and epiphyses not completely fused from Mato Grosso, Brazil (USNM 393769 ♂) was mistakenly assigned to both *C. paranus* and to *C. milleri* by Eger (2008: 405).

Handley (1966: 772) identified a series of a small-median *Cynomops* from the Canal Zone region in the 1960s during a survey of the mammal's ectoparasites in Panama as *Cynomops planirostris* due to a more evident whitish band on the mid-ventral region, and later the same series was identified as *C. paranus* at the NMNH and as *C. greenhalli* at AMNH. Two additional specimens were collected by Raùl Rodriguez, Elias Bader and Thomas Sattler in 2004 and 2012. This new taxon was recovered as sister group to *C. mexicanus* by Moras *et al*. (ms) and is described here as a new taxon:

***Cynomops* sp. 1**, new species

Figures 4–6, 8

Molossops planirostris Handley, 1966: 772; Simmons and Voss, 1998:150; part, not Peters, 1865

Molossops paranus Simmons and Voss, 1998:150; part, not Thomas, 1901

Cynomops paranus Peters *et al*. (2002): 1109; part, not Thomas, 1901

HOLOTYPE: An adult male (STRI 80) collected in a house ("casa 271"; Fig. 7A) at Gamboa Ridge (09°07'01"N, 79°41'38"; 53 m), municipality of Colon, Panama, by Raùl Rodriguez,

Elias Bader and Thomas Sattler (original number: 20120805_80) on August 5 2012. The holotype is a fluid preserved with the skull removed.

MEASUREMENTS OF THE HOLOTYPE: FA 36.10, E 14.27, TL 33.08, HF 8.11, GLS 18.37, POB 4.52, ROS 7.89, C-C 5.42, ZB 12.68, BB 8.71, MB 12.81, MTRL 7.47, BM 8.42, CIL 18.91, ML 13.51, Weight 19 g.

PARATYPES: A young female (STRI 589) collected in Gamboa (09°07'01"N, 79°41'38"; 53 m), municipality of Colon, Panama, by Kirsten Jung on September 2 2004; and an adult female series deposited at NMNH (319084 – 88) from Pacora, province of Panamá, Panama (09°05'N, 79°17'W and 09°00'N, 79°35'W; 29 m), collected by Charles. M. Keenan in June 20, 1961 (Table 3).

Figure 7. Houses used as shelter by individuals of *C. freemani*, in Gamboa, Colon, Panama. (A) "Casa 71" where the holotype was collected. (B) Old church occupied by other individuals of *C. freemani*. Photograph by Elias Bader.

DISTRIBUTION: *Cynomops* sp. 1 is known from both the Atlantic (Caribbean Sea) and Pacific coasts of the Canal Zone region in Panama (Fig. 3).

DIAGNOSIS: *Cynomops* sp. 1 is similar externally, and in size to *C. milleri* and to *C. greenhalli* and most of the measurements overlaps (males: FA 36.00–36.10, n=2; GLS

17.65–18.37, n=2; females: FA 32.64–33.50 n=10; GLS 16.37–17.00 n=10; Table 3) but the skull is relatively long and narrow (males: MTRL 7.46–8.42, POB 4.35–4.52; females: MTRL 7.38–8.03, POB 4.19–4.36; Figs. 4B, E). The postorbital constriction of *Cynomops* sp. 1 is narrow and forms a smooth angle with the elongated rostrum; the dorsal margin of the external nares is not deeply emarginated; the supraoccipital is straight and extended in lateral view; the basisphenoid pits are present but weakly developed; the mandible is gently curved along its length; and the first lower premolar (p4) is a half or less of the height of the second lower premolar (p5).

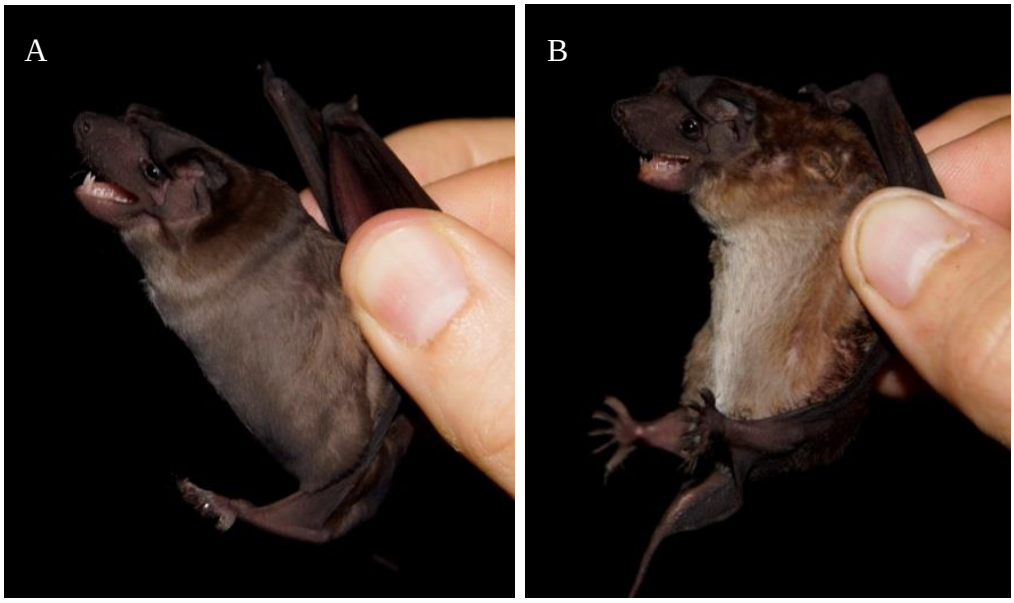

Figure 8. Photograph of (A) a male *Cynomops* sp. 1 (PN 73) and (B) a female (PN 299), both captured at Gamboa, Colon, Panama by Raùl Rodriguez, Elias Bader and Thomas Sattler . Photograph by Elias Bader.

DESCRIPTION: *Cynomops* sp. 1 has reddish-brown to dark-cocoa brown dorsal pelage, with a slightly paler venter with a whitish portion from the throat to mid-ventral region varying from weak to conspicuous (Fig. 8). The pelage is silky, and the dorsal fur is short (3 mm in length, taken on the level of the scapular area); individual dorsal hairs are bicolored, with

the basal third of each hair pale-buff. Most specimens have also frosted silver hairs scarcely distributed on dorsal fur.

The skull has an elongated rostrum; the post-orbital constriction is narrow and smoothly angled with the rostrum (Figs. 4B, E); the dorsal margin of the external nare is not deeply emarginated (Fig. 6C); the supraoccipital is straight and extended in lateral view; the basisphenoid pits are weakly developed. The mandible is gracile, with a gently curved corpus along its length (Fig 5B, E). The first lower premolar (p4) is a half or less of height of the second lower premolar (p5), usually smaller in females. The character of having a small p4 supports the sister relationship between *Cynomops* sp. 1 and *C. mexicanus*.

COMPARISONS: *Cynomops* sp. 1 resembles *C. milleri* and *C. greenhalli*, but the skull of *Cynomops* sp. 1 is relatively longer and narrower (Figs. 4B, E). These three species can be separated from the *C. planirostris* and *C. mexicanus* by the abrupt angle formed by the rostrum with the forehead, which slopes smoothly proximal to the forehead in *C. mexicanus* and *C. planirostris*. *Cynomops* sp. 1, *C. milleri*, and *C. greenhalli* can also be separated from *C. planirostris* and *C. mexicanus* by the relatively farther location of the accessory foramen relative to the incisive foramina, forming an arrangement similar to an isosceles triangle. In contrast, these three foramina form an equilateral triangle due to their relatively close location one to the other in *C. planirostris* and *C. mexicanus*.

Cynomops sp. 1 can be distinguished from *C. mexicanus* by the presence of a median ridge on the lingual face of the second lower premolar, which is absent in *C. mexicanus*; and by the shallow fossa on the posterior squamosal bone, where the zygoma meets the braincase, which is deep in *C. mexicanus*. *Cynomops* sp. 1 can be distinguished from *C. milleri* and *C. greenhalli* by the smooth angle formed between the post-orbital

constriction and the rostrum in *Cynomops* sp. 1, sharply defined in *C. greenhalli* and *C. milleri* (Fig. 4); by the weakly developed basisphenoid pits in *Cynomops* sp. 1, absent in *C. greenhalli* and *C. milleri*; by the gracile mandible of *Cynomops* sp. 1, opposed to the massive and concave in males of *C. greenhalli* and *C. milleri* (Fig. 5); and by the smaller size of the first premolar that is a half or less of height of the second lower premolar in *Cynomops* sp. 1, while is two-thirds or more of the height of the second lower premolar in *C. greenhalli* and *C. milleri*. Interspecific genetic distances for the Cytochrome *b* mitochondrial region of *Cynomops* sp. 1 varied from 7.9% (*C. mexicanus*) to 12.3% (*C. milleri*) (Moras *et al*. ms).

NATURAL HISTORY: *Cynomops* sp. 1 is known from fragmented and anthropic habitats in the Canal Zone, Panama. Individuals caught recently, including the holotype, were found sheltering abandoned houses (Figs. 7A, B). One pregnant female was caught on 05 August 2012 and two post-lactating females on 23 August 2012.

Reid *et al*. (2000) acquired a subadult male of small-median *Cynomops* (ROM 105504) from Orellana, Ecuador and identified as *C. paranus*. Later, in 2010, four additional specimens were acquired and identified as *C. milleri* by Diego G. Tirira. In a phylogenetic analysis Moras *et al*. (ms) recovered all five individuals forming a monophyletic group, sister to *C. milleri*. Here we describe these specimens as:

***Cynomops* sp. 2**, new species

Figure 4–6, 9

Cynomops planirostris paranus Sanborn (1941: 386). Part, not Thomas, 1901

Molossops paranus Reid *et al*. (2002): 45. Part, not Thomas, 1901

Molossops milleri Tirira (2012): 225. Part, not Osgood, 1914

HOLOTYPE: An adult female (QCAZ 11788; Fig. 9A) netted on Gareno River (01°02'S, 77°22'W; 343 m), next to the Nemora´s well exploration, Huaorani territory, Napo Province, Ecuador (Figs. 10A, B), by Diego G. Tirira (original number: DTS 1150) on March 23, 2010. The holotype is fluid-preserved with skull removed.

MEASUREMENTS OF THE HOLOTYPE: FA 32.57, E 12.11, TL 27.36, HF 7.27, GLS 16.05, POB 4.68, ROS 6.97, C-C 4.46, ZB 10.91, BB 8.55, MB 10.25, MTRL 5.96, BM 7.38, CIL 15.79, ML 11.38, Weight 14.8 g.

PARATYPES: Three individuals collected at the same site of the holotype: two adult females (QCAZ 11789, 11790) collected together the holotype and a subadult male (QCAZ 117891, Fig. 9B) collected on March 23, 2010; and a subadult male (ROM 105504) collected at Estación Científica Onkone Gare, Orellana Province, Ecuador (0°02'07" N and 72°38'23" W, 195 m) by Fiona A. Reid, Mark D. Engstrom and Burton K. Lim on February 8, 1996.

DISTRIBUTION: *Cynomops* sp. 2 is known from lowlands (195–529 m a.s.l.) of northeastern South America, on the eastern slopes of the Andes in Ecuador and Colombia (Fig. 3).

Figure 9. Photograph of (A) a female *Cynomops* sp. 2 (QCAZ 11788, holotype) and (B) a male (QCAZ 11791, paratype), both captured at Gareno River, Napo, Ecuador, by Diego Tirira. Photograph by Diego Tirira.

DIAGNOSIS: A small *Cynomops* (males: FA 34.38–35.45, n=4; GLS 17.12–17.53, n=4; females: FA 31.28–32.57 n=3; GLS 15.13–16.05 n=3; Table 3); skull similar to *C. milleri* but much more gracile, with crests and process of the skull less marked (Figs. 4C, F; 5C, F). The anterior face of the lacrimal ridges slopes smoothly proximal to the forehead; the nasals are relatively short resulting in comparatively longer narial openings (deeper dorsal emargination, Fig. 6A). The post-orbital constriction forms a smoothly angle with the rostrum; the posterior border of the skull (inter-parietal region) is expanded posteriorly (Figs. 4C, F); the zygomatic process of the maxilla is reduced when in dorsal view of the skull (Figs. 4C, F); incisive foramina located closer to the accessory foramen, the arrangement of the three foramina form an equilateral triangle (Fig.6A); the mandible is gently curved along its length (Figs. 5C, F); the first lower premolar is two-thirds or more of the height of the lower second premolar.

DESCRIPTION: *Cynomops* sp. 2 has dark-cinnamon brown dorsal pelage, with a uniformly brown venter, similar or slightly paler than dorsum. The pelage is silky, and the dorsal fur is short (4 mm in length, taken at the level of the scapular area); individual dorsal hairs are weakly bicolored, almost not seen macroscopically, with the basal fourth of each hair pale-buff.

Gracile skull with the posterior border (inter-parietal region) expanded posteriorly; the post-orbital constriction forms a smoothly angle with the rostrum in dorsal view of the skull (Figs. 4C, F); the dorsal contour of external nares is deeply emarginated resulting in a comparatively longer narial opening (Fig. 6A); the zygomatic process of the maxilla is reduced and do not reach the post-orbital constriction region in a dorsal view of the skull; the anterior face of the lacrimal ridges slope smoothly proximal to the forehead; the incisive

foramina are located relatively close to the accessory foramen (Fig. 6A). There is a gracile mandible, with a gently curved ramus along its length (Figs. 5C, F). The first lower premolar is two thirds or more of the height of the second lower premolar.

COMPARISONS: *Cynomops* sp. 2 can be separated from *C. planirostris* and *C. mexicanus* by the patterns of ventral pelage coloration, which is only slightly paler than dorsum, while is much paler than dorsum in *C. mexicanus* or present an evident whitish band on the mid-ventral region in *C. planirostris*; and by the gracile mandible in *Cynomops* sp. 2, opposed to the massive and concave in males of *C. mexicanus* and *C. planirostris* (and also *C. milleri* and *C. greenhalli*). *Cynomops* sp. 2 can be distinguished from *C. greenhalli*, *C. milleri*, and *Cynomops* sp. 1 by the smoothly angle formed by the rostrum and the forehead, which is abrupt in *C. greenhalli*, *C. milleri*, and *Cynomops* sp. 1 (Fig. 5); by the relatively closer location of the accessory foramen relative to the incisive foramina, forming an arrangement similar to an equilateral triangle, which forms an isosceles triangle due to the posterior location of these three foramina in *C. greenhalli*, *C. milleri* and *Cynomops* sp. 1 (Fig. 6). *Cynomops* sp. 2 can also be separated from *C. milleri* by the reduced zygomatic process of maxilla, which is longer and may reaches the post-orbital region in *C. milleri*; by the external nares deeply emarginated, which is less deep in *C. milleri* (Fig. 6); and by the posterior expansion of the inter-parietal region, which is less developed in *C. milleri* (Figs. 4, 5). Interspecific genetic distances for the Cyt *b* gene of *Cynomops* sp. 2 varied from 4.6% (*C. milleri*) to 12.5% (*Cynomops* sp. 1) (Moras *et al*. ms).

NATURAL HISTORY: The specimens from Ecuador were collected in lowland evergreen pristine forests. Two non-pregnant lactating females were caught on 24 march 2010.

Figure 7. Exact location in Gareno River, Napo, Ecuador, where the series of *Cynomops* sp. 2 (QCAZ 11788–11791) were captured. Photography by Diego Tirira.

4. Discussion

Cynomops paranus has been considered a widespread species ranging from Panama to northern Argentina, and *C. milleri* restricted to the type locality in northern Peru and Venezuela (Reid *et al*., 2000; Peters *et al*., 2002; Eger, 2008). However, based on molecular, morphometric and discrete morphological characters we suggested *C. paranus* as junior synonym of *C. planirostris* and recognized *C. milleri* as a valid species distributed on northern and eastern South America. Two additional species were described based on the material previously identified as *C. paranus*, *Cynomops* sp. 1 restricted to Canal Zone region in Panama, and *Cynomops* sp. 2 ranging from Colombia to Ecuador on the eastern slopes of the Andes.

Cynomops sp. 1 represent the second bat recently discovered from the survey of the mammal's ectoparasites in Panama in 1960´s. The first was the phylostomid bat *Vampyressa elisabethae* Tavares *et al*. (2014), and both species seems to be endemic to the

Canal Zone Region. Both the gap where these species were first collected and old age of description (~50 years ago) highlights how incomplete is our knowledge regarding the diversity presented by the collections around the world (Kemp, 2015).

On the other hand, the current available material of *Cynomops* is poorly represented in collections and do not indicate the complete range of variation for these sexually dimorphic taxa, hindering the taxonomic comprehension of the group. Simmons and Voss (1998) and Peters *et al*. (2002) commented about the difficulties in distinguish *C. milleri* from *C. greenhalli* as the smallest individuals of *C. greenhalli* overlap with *C. milleri*. As *C. greenhalli* has a broad distribution, ranging from Panama to Ecuador, Venezuela, Trinidad and Tobago, on both sides of Andes, it is probably that it also may represent a species complex and a taxonomic scrutiny is required.

Key to species of the genus *Cynomops*

1. Large size, forearm longer than 41 mm; greatest length of skull in males more than 20.0 mm, and in females more than 18.5 mm; ventral pelage coloration only slightly paler than dorsum……..……..……...……...……2

1’. Small size, forearm shorter than 40.0 mm; greatest length of skull in males less than 19.0 mm, in females less than 18.0 mm; ventral pelage coloration may be much paler in, at least in part of the ventral axis of the body.…….……...……3

2. Skull robust (males: GLS 22.30–24.71 mm; females: 19.15–20.96 mm); anterior face of the lacrimal ridges forming an abrupt angle with the forehead; incisive foramina located closer to the accessory foramen, incisive and accessory foramina arranged in the shape of an equilateral triangle when viewed from above; massive and concave mandible in males; shallow and wide trigonid on m1…….....……*C. mastivus*

2’. Skull gracile and small (males: GLS 19.94–22.26; females: 18.39–20.49); anterior face of the lacrimal ridges sloping smoothly to the forehead; accessory foramen separated from the incisive foramina by a large gap; incisive and accessory foramina arranged in the shape of an isosceles triangle; gracile mandible in males; deep and narrow trigonid on m1……...……*C. abrasus*

3. Rostrum relatively low, with anterior face of the lacrimal ridges sloping smoothly to the forehead (Fig. 5C, F); incisive and accessory foramina arranged in the shape of an equilateral triangle when viewed from above..……..……...…….4

3’. Rostrum relatively high, with anterior face of the lacrimal ridges forming an abrupt angle with the forehead (Fig. 5A, B, D, E); incisive and accessory foramina arranged in the shape of an isosceles triangle…….....……..…….....……...6

4. Large size (males: FA 36.80–37.05 mm, GLS 17.80–18.78 mm; females: FA 33.02–36.30 mm, GLS 15.87–17.57 mm); venter paler than dorsum; median ridge on lingual face of the second lower premolar vestigial or absent; deep fossa in the posterior squamosal bone, where the zygoma meets the braincase ……...…….*C. mexicanus*

4’. Small size (males: FA < 36.50, GLS < 17.50; females: FA < 35.00, GLS < 16.20); median ridge on lingual face of the second lower premolar well-developed; shallow fossa in the posterior squamosal bone, where the zygoma meets the braincase……..…...…5

5. Bicolored dorsal hairs, with the basal half colored pale-buff; ventral pelage coloration much paler than dorsum, at least at the gular and mid-ventral region whitish or pale-buff colored .....*C. planirostris*

5’. Dorsal hair with only one-fourth basal pale-buff and darker ventral coloration without paler or whitish marks …….……*Cynomops* sp. 2

6. Rostrum relatively narrow (males: POB 4.35–4.52 mm; females: 4.19–4.36 mm); gracile and relatively straight mandible in males (Fig. 5B, E); first lower premolar, p4, is a half or less of height of the lower second premolar, p5……...……*Cynomops* sp. 1

6’. Rostrum relatively broad (POB: males > 4.50 mm; females > 4.30 mm); massive mandible with a concave corpus along its length in males (5A, D); first lower premolar, p4, is two-thirds or more of the height of the lower second premolar, p5.……...……...…7

7. Smaller size (males: FA 34.00–37.00 mm, GLS 16.71–18.23 mm; females: FA 30.30–35.00 mm, GLS 15.49–16.51 mm); relatively short rostrum (MTRL Males: 6.61–6.87 mm; females: 5.38–6.29 mm); basal half of each dorsal hair pale-buff colored; nasal process of the premaxilla reduced with lateral margin of the external nares concave……*C. milleri*

7’. Larger size (males: FA 35.00–39.7 mm, GLS 17.37–19.23 mm; females: FA 33.40–38.28 mm, GLS 15.91–17.82 mm); long rostrum (MTRL males: 6.79–7.67 mm; females:

6.22–7.05 mm) basal third of each dorsal hair pale-buff colored; nasal process of the premaxilla well-developed, with lateral margin of the external nares straight....*C. greenhalli*

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Appendix

Examined material: ♂ = male, ♀ = female.

Cynomops planirostris (total 143) – **French Guiana**: CAYENE: ZMB 2513 (♂). **Guyana**: BERBICE: USNM86907 (♂); EAST DEMERARA-WEST COAST BERBICE: Rio Cuyuni, Hyde Park: FMNH22486 (♂), 22487 (♂); UPPER TAKUTU-UPPER ESSEQUIBO, RUPUNINI: Ruawau River, Raa Wau: ROM37955 (♂), 38551 (♀); Warimure, Weri More, Quash Wau Area, 12 mi NE Dadanawa: ROM44426 (♂), 52235(♂); Kataliriwau River, Katalier Wau, 20 mi E of Dadanawa: ROM65368 (♂); Kuitaro River, 30 mi E of Dadanawa: ROM71677 (♀); Kuma River, 5 mi E, 5.5 mi S of Lethem, Kanuku Mountain: ROM97854 (♀). **Colombia**: AMAZONAS: Letícia: ROM70999 (♀), 62577 (♂); BOYACA: Pore: ROM62520 (♂). **Venezuela**: APURE: San Fernando De Apure: USNM374031 (♂). BOLIVAR: Hato La Florida, 47 Km ESE Caicara: USNM405830 (♀); 2km NE Maripa: KU119090 (♂). AMAZONAS: San Juan, 163 Km ESE Pto. Ayacucho, Rio Manapiare: USNM409498 (♀), 409499 (♀), 409501 (♀), 409503 (♀), 409504 (♀), 409505 (♀), 409508 (♀), 409509 (♂), 409511 (♂), 409512 (♀), 409513 (♀), 409514 (♀), 409515 (♂), 409516 (♀), 409517 (♀), 409518(♀), 409519 (♀), 409522 (♀), 409524 (♀), 409525 (♀), 409552 (♀), 409553 (♀), 409554 (♀), 409555 (♂), 409556 (♂), 409557 (♀), 409558 (♀), 409559 (♀), 409561 (♂), 409562 (♂), 409563 (♂), 409564 (♀), 409565 (♂), 409566 (♂), 418382 (♀), 418384 (♀), 418387 (♀), 418388 (♀), 418398 (♀), 418402 (♀), 418406 (♀), 418407 (♀), 418408 (♀), 418409 (♀), 418410 (♀), 418411 (♀), 418414 (♀), 418416 (♀), 418417 (♀), 418418 (♀), 418419 (♀), 418420 (♀), 418421 (♀); San Carlos De Rio Negro: USNM560638 (♂), 560639 (♂), 560640 (♀), 560641 (♀), 560687 (♂), 560688 (♀), 560689 (♀). MONAGAS: Hato Mata De Bejuco, 55 Km SSE Maturin: USNM441842 (♀), 441843 (♀), 441844 (♂), 441845 (♀), 441846 (♀). BOLIVAR: Maripa, Sucre: AMNH17096 (♀), 17097 (♀). **Bolivia**: BENI: San Joaquin: FMNH96038 (♀). SANTA CRUZ: Chiquitos, Robore: AMNH260261 (♂). **Brazil**: SÃO PAULO: Sales, Fazenda Esplanada: ROM77311 (♂); Estação Ecológica de Caetetus: ROM111056 (♀); Urupês: AMNH236221 (♂). MATO GROSSO: Serra do Roncador, 264 Km N Xavantina: USNM393768 (♂), 393769 (♂). MATO GROSSO DO SUL: Urucum: FMNH26772 (♂). MARANHÃO: Buriti: AMNH37043 (♀), 37049 (♀). PERNAMBUCO: Estação Ecológica do Tapacura, São Lourenco da Mata: USNM555727 (♂). AMAZONAS: Tefé: USNM531145 (♀); Rio Negro, Miripinima, Airo: AMNH79731 (♀),

79733 (♀); Rio Madeira, Rosarinho: AMNH92254 (♀); Vila Bela, Imperatriz, Parintins: AMNH92971 (♂); Rio Amazonas, Itacoatiara: FMNH20640 (♀), 20649 (♂), 20650 (♀). PARÁ: Rio Tapajós, Igarapé Brabo: AMNH94642 (♀), 94644 (♀), 94646 (♂), 94648 (♂), 94649 (♀), 94650 (♀), 94652 (♂), 94653 (♀); Rio Tapajós, Aramanay: AMNH94633 (♀), 94636 (♀); Rio Tapajós, Caxiricatuba: AMNH94639 (♂), 94640 (♂); Rio Amazonas, Faro: AMNH93879 (♂), 93880 (♀), 93882 (♀), 93883 (♀), 93886 (♂). PARÁ: Santarém: MZUSP13892 (♀); Santarém, Vila Alter do Chão: INPA3935 (♂), 3959 (♀), 3960(♀); Rio Tapajós, Fordlandia: MZUSP17589 (♀). RONDÔNIA: Vila Veneza: INPA6005 (♂), 6006 (♀), 6007 (♀), 6008 (♀). **Paraguay**: ALTO PARAGUAI: Fuerte Olimpo: AMNH234455 (♀), 234456 (♂), 234457 (♂), 234458 (♀), 234459 (♀); Estancia Guyra Toro: TTU116566 (♀). CORDILLERA: Juan de Mena: USNM552738 (♀). CANINDEYU: Reserva Natural del Bosque Maracayu: TTU116561 (♀). CONCEPCIÓN: Parque Nacional Serrania de San Luis: TTU80261 (♀). MISIONES: Refugio Yabebyry-Sta. Ana: TTU80330 (♂), 80331 (♀). NEEMBUCO: Estancia Yacare: TTU80591 (♀). PRESIDENTE HAYES: Estancia Samaklay: TTU80500 (♀). BOQUERÓN: Base Naval Pedro P. Peña: TTU79997 (♀).

Cynomops paranus (total 26) –**Venezuela**: BOLÍVAR: El Manaco: USNM387745 (♂). **French Guiana**: PARACOU: Near Sinnamary: AMNH267535 (♂); SAUL: KU135372 (♂), 13373 (♀), 135374 (♀), 135375 (♀).**Guyana**: UPPER DEMERARA-BERBICE: Arampa, 3 mi S of Ituni: ROM57375 (♂), 57337 (♀), 57338 (♂), 57505 (♀). 3.5 mi E of Ituni, Cambridge's Camp: ROM62411 (♂). 3 mi W of Ituni Village, Rock Stone Road: ROM69181 (♀). UPPER TAKUTU-UPPER ESSEQUIBO: Rupununi, Kuitaro River: ROM32426 (♀). POTARO-SIPARUNI: 38 Mile Camp, 35 km SW of Kurupukari, Iwokrama Reserve: ROM108465 (♀), 108466 (♀); 's' Falls, Siparuni River, 50 km Wsw of Kurupukari, Iwokrama Reserve: ROM109178 (♀). ESSEQUIBO ISLANDS-WEST DEMERARA: Shanklands: ROM115522 (♂), 115523 (♂), 115524 (♀), 115525 (♀), 115579 (♀). **Suriname**: SIPALIWINI: Bakhuis: ROM117009 (♀), 117097 (♂). **Brazil**: AMAZONAS: Manaus, Rio Negro, Igarapé Cacao Pereira: AMNH79745 (♀). PARÁ: BMNH 1.7.11.15(♂). Santarém, Alter do Chão: INPA3958 (♂).

Cynomops milleri (total 2): **Peru**: LORETO: Yurimaguas: FMNH19652 (♀). **Venezuela**: BOLÍVAR: El Manaco, 59Km SE El Dorado, Km74: USNM387744 (♀).

Cynomops greenhalli (total 28) – **Panama**: DARIEN: Tacarcuna Village Camp: USNM310264 (♂), 310265 (♀), 310266 (♂), 310267 (♀), 310268 (♀), 310269 (♀), 310270 (♀), 310271 (♀), 310272 (♀), 310273 (♂), 310274 (♀), 310275 (♂); Jaque, Rio Imamadol: USNM363108 (♀).BOCAS DEL TORO: Isla San Cristobal: USNM449875 (♂). **Belize**: AMNH274123 (♂). **Colombia**: CUNDINAMARCA: Girardot: ROM54534 (♀); Melgar: ROM65474 (♂). **Venezuela**: ARAGUA: Ocumare de la Costa, 3km S: USNM510579 (♂). SUCRE: Tacal, 1Km SSW Cumana: KU119087 (♀), 119088 (♀). **Trinidad and Tobago**: TRINIDAD: Saint George County, Port of Spain: AMNH175326

(♂), 176285 (♀), 176286 (♀), 207071 (♀). **Ecuador**: LOJA: Zapotillo, Via Paletillas: QCAZ3334 (♀).GUAYAQUIL: Bosque Protector Cerro Blanco: LEOCAN243 (♂), 244 (♀). **Brazil**: AMAZONAS: Rio Preto da Eva, Reserva Galvão: INPA2658 (♂).

Cynomops mexicanus (total 7) – **Mexico**: JALISCO: 7 1/2mi SE, tecomates, 1500ft: KU108609 (♂), 108610 (♀), 111621 (♂). GUERRERO: Chilpancingo, 3 Km N Agua del Obispo: KU99741 (♀). OAXACA: 20 mi S, 5mi E Sola de Veja, 4800 ft: KU99747 (♀). NAYARIT: El Casco, Rio Chilte: USNM511544 (♀); Arroyo De Jiguite, Rio Santiago: USNM523453 (♀).

Cynomops freemani (total 15): **Panama**: PANAMA: Pacora: USNM319084 (♀), 319085 (♀), 319086 (♀), 319087 (♀), 319088 (♀); Ciudad de Panamá: AMNH183161 (♀). CANAL ZONE: Fort Clayton: USNM317627 (♀), AMNH183865 (♀); Fort Amador: USNM396481 (♂). Miraflores Locks: USNM312114 (♀); Balboa, La Boca: AMNH183160 (♂), 183163 (♀); Cocoli: AMNH183168 (♂). COLON: Gamboa: STRI 80 (♂), 589 (♀).
Cynomops waoranii (total 9): **Ecuador**: NAPO: Gareno: QCAZ11788 (♀), 11789 (♀), 11790 (♀), 11791(♂); Parque Nacional Yasuni, Onkone Gare, 38 km S of Pompeya Sur: ROM105504 (♂). **Colombia**: NORTE DE SANTANDER: Cucuta: FMNH51450 (♂), 51451 (♂), 51452 (♂). PUTUMAYO: Mocoa: ROM41479 (♂).

SÍNTESE

Os resultados obtidos a partir desse trabalho revelam que o uso de múltiplas abordagens, como a biologia molecular e a taxonomia, são ferramentas úteis para o estudo e compreensão de táxons crípticos. Com uma densa amostragem de táxons e caracteres (morfológicos e moleculares) abrangendo grande parte da distribuição conhecida para *Cynomops*, um novo cenário evolutivo é proposto para o gênero, com três novas linhagens descobertas. Dentre essas, uma originou a revalidação e redescrição de *C. mastivus*, e as outras duas resultaram na descrição de duas novas espécies, *Cynomops* sp. 1 e *Cynomops* sp. 2. Além disso, o parafiletismo de *C. milleri* e *C. paranus*, aliado à análise de caracteres morfológicos, contribuíram para corroborar a validade de *C. milleri* e sugeriram *C. paranus* como sinônimo júnior de *C. planirostris*. Após essa revisão sistemática do grupo, com a descrição e revalidação de táxons, a diversidade de *Cynomops* teve um aumento considerável, e hoje contabiliza em oito espécies distribuídas na região Neotropical.

Num contexto evolutivo, as relações de parentesco aqui propostas sugerem uma origem centro-americana, visto que *C. mexicanus* e *Cynomops* sp. 1, ambas da América Central, formam um clado basal, mas uma maior diversificação na América do Sul, com a maioria das espécies derivadas ocorrendo neste continente. No entanto, é necessário um estudo específico de diversificação temporal e espacial do gênero para testar esta hipótese.