DNA barcoding of Neotropical mammals, advances of Colombia at a regional scale, and the development of a reference library in the Northern lowlands.

MAURICIO SERNA-GONZÁLEZ*, VALENTINA GRISALES-BETANCUR*, OSCAR S. ALZATE-ZAPATA*, DUVAN NANCLARES+, LUISA F. ORTÍZ+, MARTHA OLIVERA+, JUAN F. DÍAZ-NIETO*

*Departamento de Ciencias Biológicas and Grupo de Investigación BEC, Universidad EAFIT, Cr 49 No.7sur-50, Bloque 38, 050022, Medellín, Colombia
+Grupo de Investigación Biogénesis, Facultad de Ciencias Agrarias, Universidad de Antioquia, Calle 67 No. 53 - 108, Medellín, Colombia.

Abstract.
Neotropical region, specially the Andes and the Biogeographic Choco hotspots, presents high mammalian diversity. Even though some efforts aiming to barcode this diversity have been conducted, they have been insect centered. Mammals have been constantly forgotten. Especially in Colombia, where just 1.7% of the mammalian diversity is barcoded, morphological variation has not been included in taxonomic reviews, resulting in inaccurate species identification. In this context a single gene approach as DNA barcoding for species discovery is not possible. Therefore, we employed an integrative approach using a thorough morphological revision, maximum likelihood topologies and distance-based clustering to generate the first reference database for Colombian mammals. Here we present 100% newly COI and CYTB sequences for Colombia, including 9 new BINS in BOLD. Moreover we show high intra- and inter-specific distance variability, questioning distance-based methods as the sole source of information. We increase by four Colombian barcoded mammals and prove that an exhaustive effort is needed in order to produce informative barcodes for future applications.

Key Words.
Biodiversity hotspots, DNA barcodes, COI, CYTB, cryptic diversity, South American mammals, Barcode Index Numbers.

Introduction.

Mammals are especially diverse in the Neotropics, with 1701 known species for the region, representing 30% of the world's mammalian diversity (Reeder *et al.* 2007). This region is not only the most species-rich region in the world, but it also harbors five biodiversity hotspots (Myers *et al.* 2000). In particular, Biogeographical Chocó and the Andes are recognized within Earth's most important centers for endemism, with just 1.2% of the planet surface, harboring 50.2% of all tropical mammalian diversity (Conservation International 2013). Nevertheless, mammalian diversity remains largely unexplored, with estimates showing that as many as 7,500 species of mammals will eventually be described (Reeder *et al.* 2007). Most of this undescribed species which are categorized as "cryptic diversity" (see definition in Bickford *et al.* 2007) are likely to be restricted to areas of high endemism and threat (Reeder *et al.* 2007). In fact, 62% of continental new mammals were described primarily from South America, specifically from Brazil and the Andes (Reeder *et al.* 2007).

Northern South American mammalian diversity has been mostly studied using classical studies of skin and skull morphology (e.g. Loureiro et al. 2018b; Martins & Hubbe 2012; Velazco & Patterson 2008). Even though these methods may be sufficient to properly separate biological entities (Baker & Bradley 2006a), many unrecognized species will not be easily detectable with traditional methods (Hebert *et al.* 2003a; Reeder *et al.* 2007). Morphology alone will be even less reliable if mammalian cryptic diversity is taken into account (Reeder *et al.* 2007). Therefore, multi-disciplinary approaches have been proposed to explore and understand biodiversity (e.g. Hebert et al. 2003, Reeder et al. 2007, de Santana et al. 2019). In this context, DNA barcoding represents a fast, reliable and efficient tool not only for known biodiversity characterization, but also for species delimitation[1] (Collins & Cruickshank 2013; Hebert *et al.* 2003a, 2004; Hebert & Gregory 2005) and biodiversity monitoring (Valdez-Moreno *et al.* 2012). Sequence divergence in Cytochrome C Oxidase Subunit 1 (COI) has been proposed as sufficient to reliably discriminate between closely related species (Hebert *et al.* 2003a, 2004). DNA barcoding, although criticized (Ebach & Holdrege 2005; Will *et al.* 2005; Will & Rubinoff 2004), has been mostly accepted by the international community. The International Barcode of Life Consortium (iBOL) (https://ibol.org) is now engaged in creating, through small pieces of DNA, a digital identification system for life. However, criticisms state that a sole source of information, whether morphology or a single gene, will be deficient in the description of taxa (Ebach & Holdrege 2005; Will *et al.* 2005; Will & Rubinoff 2004). DNA barcoding will only be useful if all species have been properly barcoded, i.e. a DNA sequence has been named after a curated voucher specimen (Collins & Cruickshank 2013; Ratnasingham & Hebert 2007) in order to construct a reference database. This reference database is far from complete, especially in non-developed countries with high biodiversity (Imtiaz *et al.* 2017), hindering the proper use of DNA barcoding (Collins & Cruickshank 2013).

Even though "huge efforts are being made to fill the gaps of genetic information in Colombia" (Gonzalez-Herrera *et al.* 2019), most sequences produced in these efforts are not publicly available on BOLD (www.barcodinglife.org) (Ratnasingham & Hebert

[1] (Collins & Cruickshank 2013) suggest "distinguishing relatively crude single-locus methods such as DNA barcoding as *species discovery*, and multilocus/ integrative methods as *species delimitation*".

2007). In fact, few papers using DNA barcoding have been published in Colombia (see results), with just two of them (Guarnizo *et al.* 2015; Mendoza *et al.* 2016) including a large taxon sampling in order to create a DNA barcode reference library for Colombian biodiversity. Compared with other Latin American member nations in iBOL, with comparable levels of biodiversity, Colombia is the one that has produced the least number of COI sequences (see below).

Due to the lack of knowledge and insufficient COI sequences in database repositories for Colombian mammals, a simple barcoding study aiming species discovery is not suitable for the country. This problem is magnified by the aforementioned barcoding debates: absence of samples with sequence data from geographical proximity and the conflicting taxonomy of neotropical small mammals (Clare *et al.* 2011). Therefore, we present firstly, a review of DNA barcodes for the Neotropics, with emphasis in Colombia. Secondly, we generate the first mammalian DNA barcode study for a Colombian locality using an approach that includes multiple lines of evidence for the species identification. In particular we implement DNA barcoding, phylogenetic reconstruction, mitochondrial genetic distances, and morphological characterization. With our approach we aim to create a library of DNA sequences exceptionally curated in quality that can be used as the baseline for species identification and delimitation. Finally, discussion is made on how this multi-approach method aids in surpassing simple DNA barcoding constraints.

Methods.

DNA barcoding advances in the Neotropics.

In order to evaluate the advances in DNA barcoding studies in the Neotropics, we downloaded all records from every country in the Neotropical region (broadly defined as including Mexico, Central America and South America) from the "Public Database Portal" in the Barcode of Life Data System (BOLD) v.4 (http://www.boldsystems.org/). All non-COI and COI human sequences (family Hominidae) were excluded from all the analyses. Using this database we calculated both the relative abundance of each class (e.g., Mammalia) and the total number of COI sequences for each country. For each country we analyzed all sequences--not taking into account the taxa they represented--and a separate analysis only for mammalian sequences also including the number of species-like units (BINS) they represent. Additionally, we developed a literature search of DNA barcoding studies in Colombia using the Google Scholar engine in addition to all the papers retrieved from BOLD's "Publications" database. For Google Scholar we used all possible combinations of words: "DNA barcoding", "barcoding", "barcodes" and "Colombia". Computing, filtering and data base analysis were done using data.table package (Dowle & Srinivasan 2019) from R (R Core Team 2019).

DNA barcodes for mammals in the Northern Lowlands of Colombia.

FIELDWORK: Fieldwork was conducted between the 21st and 29th of October of 2017 by two of the authors (MS and OSA) at a Tropical Rain Forest locality in the northern lowlands of Colombia, Antioquia department, municipality of Caucasia (Fig 1). Rodents and opossums were trapped using Sherman, Victor, and Tomahawk traps (1328 traps/night) and bats were mist-netted (7776 net/h/m^2). Sampling, handling and

euthanization of specimens followed the guidelines for the use of wild mammal species established by Sikes (2016). Individuals were prepared as museum specimens following Hall (1962) and Simmons and Voss (2009). Tissue samples and ectoparasites were collected and preserved in 96% ethanol and stored at -20ºC upon arrival to the laboratory.

MORPHOLOGICAL IDENTIFICATION: We morphologically identified all the collected material, initially by using recent identification keys for each mammal group: bats (Díaz *et al.* 2016; Lopez-Baucells *et al.* 2018), rodents (Patton *et al.* 2015) and marsupials (Gardner 2008a; Voss & Jansa 2009). We corroborated those initial identifications using other relevant literature that included systematic revisions, original species descriptions, or local revisionary work (see species account for references particular to each species).

TAXON SAMPLING AND LABORATORY METHODS: We obtained sequences from at least one specimen from each of the morphologically identified species, nonetheless, in those instances were a species exhibited extensive morphological variation we included additional specimens to secure sequences across all the observed variation. We extracted DNA from preserved tissue using the PureLink Genomic DNA Mini Kit (Invitrogen). Two mitochondrial protein-coding genes were PCR-amplified: the complete Cytochrome *b* gene (CYTB) and a fragment (~560 bp) of the Cytochrome C Oxidase Subunit I (COI). Amplification for CYTB was performed using the following combination of primers: MVZ05a and UMMZ04 (Jansa *et al.* 1999) for bats, didMVZ05 and did1260 (Giarla *et al.* 2010) for opossums, and Mus14095 and Mus15398 (Percequillo *et al.* 2011) for rodents. Amplifications of COI for all taxa were developed using the primer cocktail suggested by Ivanova *et al.* (2007). All primers were M13-tailed in order to improve sequencing yield (Ivanova *et al.* 2007). We PCR-amplified each of the two mentioned loci in 25 µl reactions using the thermal cycling conditions and PCR reagents described in Table S2. PCR products were visualized on a 1.5% agarose gel using a MiniBIS Pro-DNR Bio Imaging Systems. All amplification products were Sanger sequenced on an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA) in Macrogen (Seoul, Korea). Resultant chromatograms were manually edited in Geneious 11.0.2 (https://www.geneious.com) and low quality reads (i.e. reads with double peaks, without an open reading frame and/or with indels in the gene coding region) were eliminated as they may represent pseudogenes (Song *et al.* 2008). All the resultant reads were assembled and examined with reference to translated amino-acid sequences.

DNA BARCODING: Nucleotide sequences, trace files, sequence metadata, and images (skin and skull of all sequenced specimens) were uploaded to BOLD Systems (http://www.boldsystems.org/) and are accessible using BOLD's project code "MACAU" (after *Mamíferos Caucasia*). We assessed the correspondence between our species identification (using a dual approach of morphological identification and Maximum likelihood analyses, see below) and the name assigned by the DNA barcoding using the automatically Barcode Index Number (BIN) clustering (Ratnasingham & Hebert 2013). BIN is an online framework that clusters barcode sequences algorithmically (RESL, ABGD, CROP, GMYC, jMOTU) by assigning individuals to presumptive species, called operational taxonomic units (OTUs). BIN

analyses were exclusively performed for COI as the algorithm is only available for this marker.

PHYLOGENETIC ANALYSES: Because we were interested in providing a clear assignment of our haplotypes to a species, we developed independent phylogenetic analyses for each of our morphologically identified species. We implemented two independent analyses one for each marker (CYTB and COI). Each analysis included as ingroup our sequenced material of each species, all the available sequences from BOLD and Genbank from that taxon, and sequences (also downloaded from BOLD and Genbank) for all other species within the genus. In order to save computational time all duplicated reads were excluded from the analyses using the Geneious function *Remove duplicated reads* (kmer seed length=31, maximum edits=0, maximum substitutions=1). If any recognized species or subspecies was eliminated during that process, at least one sequence of each of these taxa was readded so that we could secure that all known diversity was present in the alignments. Additionally, sequences that were not properly assigned to a voucher specimen in a certified natural history museum or those tagged as unverified were eliminated from the alignments. Special emphasis was made to include all relevant sequences used by previous authors in systematic revisions. Each alignment contained as outgroup sequences of closely related taxa (see results for each species). Although, K2P is used in most DNA barcoding studies as the default DNA evolutionary model, it has been shown that the *de facto* use of K2P may hinder the results of phylogenetic reconstructions (Srivathsan & Meier 2012); therefore, the best fitting nucleotide substitution model for each analysis was determined under the Bayesian Information Criterion (BIC) in jModelTest (Posada 2008). We developed four independent ML searches in GARLI 2.0.1 (Zwickl, 2006) and evaluated nodal support based on bootstrap analyses of 1000 pseudoreplicated data sets with the same DNA substitution model as the initial searches. Bootstrap support (BS) values were summarized on the best ML tree using SUMTREES v. 4.4.0 (Sukumaran & Holder 2010). All phylogenetic analyses were implemented in CIPRES Science Gateway V.3.3 (Miller *et al.* 2010). Lastly, we estimated uncorrected genetic *p* distances within and between species using MEGA7 (Kumar *et al.* 2016). Percentage of nucleotide completeness for each of the alignments was obtained using a user-defined function (https://github.com/Valengsb/DNA-reference-libary-of-mammals-of-Caucasia-Antioquia-) in software R (R Core Team 2019).

Results.

DNA barcoding advances in the Neotropics.

DNA barcoding in the Neotropics has been insect centered with 87.1% of all COI sequences associated to the class Insecta (Fig 2A) in comparison to much smaller proportion of sequences (<3.5%) for fish, mammals, springtails, arachnids and birds (Fig 2A). Moreover, there is a great disparity in terms of number of COI sequences produced in each country. For instance, Costa Rica (ranked first in COI sequence number) has produced 500,000 sequences more than Argentina (second country in number of DNA barcoding sequences), but most Neotropical countries have produced less than 5% (i.e. <31,200) of the number of COI sequences from Costa Rica. A similar scenario occurs if just mammalian COI sequences are taken into account, not only in

terms of sequence number but also in the number of species-like units barcoded. Most available barcodes for Neotropical mammals have been produced by few countries (Guyana, Mexico, Ecuador and Suriname) which collectively have produced 45% of all the mammalian COI sequences. Other countries—even with high mammalian biodiversity—have extremely low numbers of available COI sequences (e.g. Perú and Colombia [n=10]) (Fig 2D). This low sequence number influences the number of species-like units (i.e. BINs) that have been generated. For instance, Mexico has 410 mammalian BINs within 5,162 sequences, while just 7 BINs have been published for Colombia (Fig 2D). Additionally, in terms of publications, 47 papers have been published in Colombia using DNA barcoding (see Table S3 for references) most of which are insect-related (i.e. 66%) and no single paper has been produced particularly for mammals (Fig. 2B and Table S3).

DNA barcodes for mammals in the Northern Lowlands of Colombia.

We obtained a total of 148 sequences (75 for CYTB and 73 for COI), representing 25 morphologically identified species from 81 specimens. The most diverse order was Chiroptera with 20 species, followed by Didelphimorphia with 3 and Rodentia with 2 species. Based on COI sequences, a total of 22 BINS were obtained, 9 of which are new public BINS to BOLD (see Table S1). All COI and CYTB sequences represented the first molecular data for their corresponding species for Colombia. Intra- and inter-specific uncorrected *p* distances are presented in Table 2 and are discussed accordingly in subsequent accounts.

Species account.

The following account includes all the species recognized in the present study using our multiple lines of evidence: morphology, phylogenetic analyses, mitochondrial distances, and DNA barcodes. We always introduce each species with the number of recognized species in its genus (including the corresponding author) and the number of species occurring in Colombia. We always present the authors we follow for the morphological identification and we only make comments morphology-related if we find any difference with respect to what has been described for that particular species. We present a brief analysis of the multiple lines of evidence for the species identification presented. Results of the BIN analyses and the novelty of the obtained sequences for Colombia are presented under the section “Molecular data remarks”. Finally, “Phylogenetic analysis” section includes (always in the same order) the following information for each mitochondrial marker: number of ingroup sequences, best-fitted DNA evolution model implemented in the phylogenetic reconstructions, outgroup species, and percentage of nucleotide completeness.

<u>Didelphimorphia.</u>

Caluromys lanatus
Voss and Jansa (2009) report 3 extant species for the genus *Caluromys*, two of them occurring in Colombia: *C. lanatus* and *C. derbianus* (Ramírez-Chaves *et al.* 2016). We collected a single individual corresponding to a juvenile (dp3 in place and unerupted M4) which is identified as *C. lanatus* following morphological characters proposed by Voss and Jansa (2009) and Gardner (2008a). Our phylogenetic reconstruction shows our haplotypes (for COI and CYTB) as part of a strongly supported haplogroup that

includes other sequences of *C. lanatus* (Fig 3B, A respectively). This monophyletic group has an intraspecific uncorrected p-distance of 1.9% for COI and 1.8% for CYTB. Moreover, uncorrected interspecific genetic *p*-distance is 8.5% for COI and 11.6% for CYTB. Based on morphology, sequence monophyly, and mitochondrial sequence distances we identify our specimen and associated sequences as part of the species *C. lanatus*.
Molecular data remarks: Our COI sequence created a new BIN (BOLD:ABY0655) where it currently stands as the only sequence. Both COI and CYTB sequences are the first for this species in Colombia.
Phylogenetic analysis: COI: 8, GTR+Γ, *Didelphis marsupialis*, 100%; CYTB: 6, GTR+I, *Didelphis marsupialis*, 100%.
Vouchers associated to sequenced material: JFD_01290.

Didelphis marsupialis
The genus *Didelphis* comprises 6 species (Voss & Jansa 2009), two of them occurring in Colombia (Ramírez-Chaves *et al.* 2016). Our only specimen from this genus was unequivocally identified as *D. marsupialis* following morphological traits reported by Voss and Jansa (2009). Our COI alignment included sequences for all the species of the genus *Didelphis*, except for *D. albiventris*. Our haplotype forms a well-supported monophyletic group with other COI sequences from this species (Fig 4). The intraspecific uncorrected *p*-distance is small (0.73%) relative to the uncorrected *p*-distance (2.85%) exhibited with its sister clade (*D. aurita*). Although no CYTB sequence was recovered for this species, morphology and COI analyses provide sufficient support to use the name *D. marsupialis* for this individual.
Molecular data remarks: Our sequence is part of a BIN (BOLD:AAA7109) associated to *Didelphis marsupialis*. This is the first COI sequence of the species for the country.
Phylogenetic analysis: COI: 15, HKY+Γ, *Philander frenatus,* 99.98%; CYTB: No sequence data were recovered for this species.
Vouchers associated to sequenced material: JFD_01318.

Marmosa (Exulomarmosa) isthmica
For the genus *Marmosa*, Voss et al. (2014) report 19 species, 7 of which are occurring in Colombia (Ramírez-Chaves *et al.* 2016). We collected 5 individuals that largely follow the morphological characters of *M. isthmica* described Rossi, Voss and Lunde (2010), nonetheless, they exhibit some variation here described: 1) four individuals (JFD_01263, JFD_01261, JFD_01262, JFD_01293) have a dark median stripe that extends from the rhinarium to between the eyes, a character observed only in *M. ruba*; 2) all of our material have small ears (mean = 21mm) in contrast to larger ears (25-26mm) reported for the species; 3) the temporal ridges of all five specimens converge posterior to the postorbital constriction but immediately diverge in the middle of the temporal bone (Rossi et al., 2010: Fig 12B), this is opposed to what has been described for the species (temporal ridges that converge posteriorly). Our CYTB phylogenetic reconstruction includes all the sequences from the most recent systematic revision for the genus (Voss et al., 2014) and therefore provide an ideal scenario for the species identification. Our CYTB haplotypes show little variation among them and form a strongly supported clade with the other available sequences of the species (Fig 5A). Although our CYTB haplotypes are slightly divergent with respect to the other haplotypes of the species, the observed uncorrected intraspecific distance (3.97%) falls within the observed variation for the species of the genus (Voss et al., 2014: Appendix 2). Our COI sequences are part of a strongly supported clade

and represent the first for this species (Fig 5B). Despite the observed morphological and mitochondrial variation of our material, most other morphological characters and the CYTB phylogenetic reconstruction provide evidence to identify our material as *M. (Exulomarmosa) isthmica*.
Molecular data remarks: Our COI sequence data clustered within BIN (BOLD:ADK5609) associated to the name *Marmosa isthmica*. Even though BIN BOLD:ADK5609 has already 2 other members, this sequences are not public. Therefore, all of our haplotypes, for both markers, are new for Colombia and those for COI represent the first published sequences for the species.
Phylogenetic analysis: COI: 18, GTR+Γ, *Caluromys philander,* 99.5%; CYTB: 35 (all available sequences of the subgenus *Exulomarmosa*), GTR+I+Γ, *Marmosa (Eomarmosa) lepida*, 86.7%.
Vouchers associated to sequenced material: JFD_01237; JFD_0262; JFD_01263; JFD_01293; JFD_01294; JFD_01296.

Chiroptera.

Molossidae.

Molossops temminckii
We follow the recognition of the genus *Molossops* with only two species, *M. neglectus* and *M. temminckii* (Gregorin & Cirranello 2016), with both species found in Colombia (Ramírez-Chaves *et al.* 2016). For these two species, their morphological characters have been clearly defined (Gregorin & Cirranello 2016) and our single specimen follows the morphological characters of the species *M. temminckii*. Both COI and CYTB sequences are part of strongly supported monophyletic groups of haplotypes of *M. temminckii* distributed in the lowlands east of the Andes (Cis-Andean) (Fig 6B, A respectively). Based on the available evidence, we confidently allocate our material under the name *M. temminckii*.
Molecular data remarks: Our sequences are the first with a trans-Andean distribution and are also the first for Colombia. COI sequence founded a new BIN (BOLD:AEA3427). This BIN has a 3.21% p-distance with its nearest neighbor (BOLD:AEA3149).
Phylogenetic analysis: COI: 9, HKY+Γ, *Molossus coibensis,* 99.98%; CYTB: 5, GTR+I, *Molossus coibensis,* 100%.
Vouchers associated to sequenced material: JFD_01220.

Molossus
The genus *Molossus* is one of the most diverse and widely distributed genera of free tailed bats (Loureiro *et al.* 2018b; a). Therefore its systematics has been in constant change, with not only new species being recently described (González-Ruiz *et al.* 2011; Loureiro *et al.* 2018b) and others prone to description, but also several subspecies forming well supported monophyletic groups (Loureiro *et al.* 2018b; a). Following recently morphological (Loureiro *et al.* 2018a) and molecular (Loureiro *et al.* 2018b) reviews there are 10 recognized species of *Molossus*, 6 of them occurring in Colombia (Ramírez-Chaves *et al.* 2016). We captured and sequenced 9 specimens that were morphologically identified within this genus, representing 3 species, i.e. *M. rufus, M. molossus and M. sp.* following Loureiro, Gregorin and Perini (2018a).

Molossus molossus

Recently published taxonomical reviews (Loureiro *et al.* 2018b; a) have clarified the diagnostic characters for *M. molossus.* Here, interspecific morphological differences are based on presence/absence characters rather than just on size variation (Díaz *et al.* 2016; like in Gardner 2008a), making identification more reliable. Following these reviews, we identified one captured specimen as *M. molossus*. However, this old individual has a high tooth wear, hindering the correct identification of character 10 (i.e. orientation of the upper incisors) (Loureiro *et al.* 2018a). In spite of this, all other diagnostic characters were normal to *M. molossus*. Both COI and CYTB sequences were produced for this individual, being the first sequences for Colombia. Regarding ML, COI gene tree includes the three *M. molossus* subspecies identified by Loureiro, Lim and Engstrom (2018b). However, and similar to Loureiro, et al. (2018b)'s results, monophyly of *M. molossus molossus* has low BS values (Fig 7B). Notwithstanding, our sequence is more closely related to sequences identified by Loureiro et al. (2018b) as *M. molossus molossus* than to any other sequences. Similarly, our CYTB sequence clusters within a not well supported clade of *M. molossus molossus,* i.e. Clade A2 in Lindsey and Ammerman (2016) (Fig 7A). We included sequences for COI and CYTB retrieved from the same museum voucher in order to improve molecular identification. Low uncorrected p-distances were observed for both genes within *M. m. molossus* group and between closely related species. For COI intraspecific distance was 0.6% and with its more closely related group (*M. sp.* from Colombia, see below) 0.9%. For CYTB, intraspecific uncorrected p-distance was 1.3% and with its more closely related group, the same as in COI, 1.7%. Even though *M. molossus molossus* doesn't form a well-supported monophyletic group in either tree, we argue that this sequence belongs to this taxon as not only clusters with conspecific sequences recently published in taxonomic reviews, but also presents the morphological diagnostic characters for *M. molossus.* Moreover, COI sequence clusters within BIN: BOLD:AAA2454 of *M. molossus*.

Molecular data remarks: Both COI and CYTB sequences are the first ones for Colombia. COI sequences cluster within a BIN assigned to *M. molossus.*

Phylogenetic analysis: COI: 346, HKY+I+Γ, *Promops centralis*, 96.77%; CYTB: 79, GTR+I+Γ, *Eumops glaucinus*, 62,8%.

Vouchers associated to sequenced material: JFD_01217

Molossus rufus

Following recent taxonomic reviews (Loureiro *et al.* 2018b; a), we identified five captured specimens (3 females and 2 males) as *M. aztecus,* yet this species is not reported for Colombia (Ramírez-Chaves *et al.* 2016). Both COI and CYTB sequences were produced for all five specimens. However, no sequences for *M. aztecus* was found for COI and only one was found for CYTB in NCBI, which was uploaded by Livia Oliveira Loureiro in 2018 but not included in her most recent reviews (Loureiro *et al.* 2018b; a). All our CYTB sequences form a monophyletic cluster with high support value (84) with *M. aztecus* sequence (Fig 7A). Nonetheless, this well supported group lies within *M. rufus* poorly supported cluster, described by Lindsey and Ammerman (2016). Additionally, all our COI sequences form a low supported monophyletic group with sequences identified by Loureiro, Lim and Engstrom (Loureiro *et al.* 2018b) as *M. rufus* (Fig 7B). Our specimens morphologically differ with *M. rufus* mainly in size, with forearm (mean: 39.9mm), maxillary toothrow (mean: 5.1mm) and palatal length (mean: 5.8mm) being below *M. rufus*'s inferior limit length range: forearm: 47.7 - 55.2mm, maxillary thoothrow: 7.5 - 8.7mm , palatal length: 6.3 - 7.8mm. Nevertheless, regarding

presence/absence characters, our specimens possess all diagnostic characters for *M. rufus* (i.e. upper incisors short and spatulated, with convergent tips; depth of the basioccipital pits moderate, without formation of crest between the basioccipital and the basisphenoid; nasal process highly developed; mastoid process facing toward the foramen magnum in posterior view) (Loureiro *et al.* 2018a). We argue that these sequences should be identified as *M. rufus* as they cluster, in both COI and CYTB gene trees, with sequences previously assigned to this taxon with low uncorrected genetic p-distance (i.e. 1.7% for CYTB and 0.81% for COI). Moreover, COI sequences cluster within BIN BOLD:ADK2184, assigned to *M. rufus*. Even though *M. rufus* is considered the largest species of *Molossus* (Loureiro *et al.* 2018b; a), not even one specimen for Colombia was analyzed in these studies. Here we give evidence of a high intraspecific morphological variation within *M. rufus.* As the *M. aztecus* sequences was not used by Loureiro, Gregorin and Perini (2018a) thus not reliable, we suggest that Colombian *M. rufus* are smaller than what was previously known and that it is urgent to sequence *M. aztecus* type in order to improve *Molossus* species identification as morphological assessment can be problematic, especially between *M. rufus* and *M. aztecus*.

Molecular data remarks: Both our markers are the first ones for the species in Colombia. COI sequences cluster within BIN BOLD:ADK2184, which has an average p-distance of 0.84%.

Phylogenetic analysis: COI: 346, HKY+I+Γ, *Promops centralis*, 96.77%; CYTB: 79, GTR+I+Γ, *Eumops glaucinus*, 62,8%.

Vouchers associated to sequenced material: JFD_01225; JFD_01227; JFD_01231; JFD_01315; JFD_01317.

Molossus sp.

Three of our *Molossus* specimens form a separate marginally supported monophyletic group. Low uncorrected intraspecific p-distances were found for both genes (i.e. 0.4% for CYTB and 0.1% for COI). In COI the most related groups, *M. coibensis* and *M. sp.* (from Venezuela and Guyana), also have a low intraspecific distance of 1.2% and 0.5%, respectively (Fig 7B). In CYTB the most related group is *M. rufus* with 1.6% interspecific uncorrected p-distance (Fig 7A). Regarding morphology, these specimens presented different traits than the other *Molossus* captured in this study. Species identification was not possible as these individuals, although been part of a monophyletic group, don't fit any species diagnosis. First of all, the three individuals don't have the same dorsal band coloration pattern. One of them (JFD_01316) with a high contrast between base and tip of dorsal hairs. This character is specific to *M. molossus.* While the other two specimens (JFD_01314, JFD_01226) don't possess a differentiable banding pattern in dorsal hairs, diagnostic character for *M. coibensis* (Díaz *et al.* 2016). Secondly, Diaz et al. (2016) dichotomous key is not consistent with Gardner (2008a). Here *M. coibensis*' forearm is less than 34.9mm while in Diaz et al. (2016) *coibensis* has a bigger forearm (>36mm). Therefore, and using Gardner et al. (2008a), our specimens (forearm mean: 38.8mm) would be included within *M. bondae* (forearm < 40mm). Lastly, the most recent morphological review (Loureiro *et al.* 2018a) didn't produce a single species identification. Our individuals vary not only in banding pattern, but also in the form of the occipital complex and the form of the upper incisors (small and spatulated for JFD_01316 and elongated with parallel tips for JFD_01314, JFD_01226), characteristics of more than two species. Additionally, Loureiro, Gregorin and Perini (2018a) diagnosis for each species was used to corroborate the identity of our individuals and none of them correspond to all characteristics of our specimens.

We conclude that these individuals should be named as *M. sp.* as they don't cluster within any previously recognized clade and don't have the diagnostic characters for any recognized species in *Molossus.* However, BIN analysis was not in concordance with our previous findings. Our sequences cluster within BIN BOLD:AAA2454 assigned to *M. molossus* (same BIN as individuals from this study identified as *M. molossus*).
Molecular data remarks: Both COI and CYTB sequences are the first produced in Colombia. BIN analysis clusters COI sequences with other sequences of *M. molossus.*
Phylogenetic analysis: COI: 346, HKY+I+Γ, *Promops centralis*, 96.77%; CYTB: 79, GTR+I+Γ, *Eumops glaucinus*, 62,8%.
Vouchers associated to sequenced material: JFD_01226; JFD_01314; JFD_01316

Phyllostomidae.

Desmodus rotundus
Desmodus rotundus belongs to a monotypic genus widely distributed in Central and South America (Martins *et al.* 2007). Cryptic diversity within this species has been widely discussed. It was first stated using CYTB by Martins et al. (2007) and Martins et al. (2009), who recognized 5 different haplogroups, and then using COI by Clare et al. (2011) that report 6 well supported clades. Additionally, by October 2019, BOLD recognizes 7 different BINS within this species. Nevertheless, we will follow Martins and Hubbe (2012) that conclude that *Desmodus rotundus* is not a group of species, instead, it is one species with high craniometric variation. Martins and Hubbe (2012), based on cranial morphology, concluded that this variation does not show any abrupt morphological discontinuities between ecological regions, thus comprising one evolutionary lineages. Our 3 captured specimens were identified as *D. rotundus* (Díaz *et al.* 2016; Gardner 2008a). Our sequences cluster with high support value with the Panamanian clade reported by Clare et al. (2011) (Fig 8). This clade has a net genetic uncorrected p-distance of 2.72% with the Central American one (Mexico and Costa Rica). Additionally, our results show a high genetic variation within *Desmodus* (intraspecific uncorrected p-distance of 4.19%), consistent with other studies (Clare *et al.* 2011; Martins *et al.* 2007, 2009). Although no CYTB sequence was obtained, we are confident that it would cluster with the Central American clade reported by Martins et al. (2009).
Molecular data remarks: These are the first Colombian COI sequences for *Desmodus* and create the eight BIN for this species (BOLD:AEA2946). This result is consistent with the high uncorrected intraspecific genetic p-distance with other *Desmodus rotundus* individuals.
Phylogenetic analysis: COI: 15, HKY+Γ, *Carollia brevicauda*, 99.95%; CYTB: No sequence data were recovered for this species.
Vouchers associated to sequenced material: JFD_01288; JFD_01289; JFD_01304

Chiroderma villosum
The genus *Chiroderma* comprises six species. Four of these are big and with conspicuous facial stripes (*C. vizottoi, C. salvini, C. doriae, C. improvisum*) and the other 2 are the smallest in the genus (*C. villosum, C. trinitatum*). Five of these species are recognized both morphologically and molecularly using CYTB by Baker et al. (1994a). More recently, Taddei and Lim (2010) based on morphological traits, describe a new species of *Chiroderma* restricted to the state of Piauí of Northeastern Brazil. In Colombia we have 3 of these species (*C. salvini, C. trinitatum, C. villosum*) (Ramírez-

Chaves *et al.* 2016). Morphologically, 5 of our specimens were readily identified as *Chiroderma villosum*. They present inconspicuous facial and dorsal stripes, forearm longer than 42mm and upper inner incisors parallel (Díaz *et al.* 2016; Gardner 2008a; Goodwin 1958). Both COI and CYTB sequences were obtained for all 5 specimens. In both genes our sequences cluster with high support value with NCBI's sequences of *C. villosum* (Fig 9B, A respectively). Additionally, not only both COI and CYTB cluster have a low intraspecific uncorrected p-distance, 1.2% and 1.1% respectively, but also present high uncorrected net genetic distance with its sister species, 7.3% and 4.3% respectively.
Molecular data remarks: Both COI and CYTB sequences are the first for this species in Colombia. COI sequences group with the only BIN available for *C. villosum* (BOLD:AAA4283), a BIN with 109 members and with an average p-distance of 1.07%.
Phylogenetic analysis: COI: 24, HKY+I+Γ, *Uroderma bilobatum*, 99.94%; CYTB: 14, HKY+I+Γ, *Uroderma bilobatum*, 96.97%.
Vouchers associated to sequenced material: JFD_01245; JFD_01248; JFD_01256; JFD_01257; JFD_01264

Chiroderma sp.
Morphologically, 2 specimens were readily identified as *Chiroderma trinitatum*. Their forearm is shorter than 42mm (mean: 36.3mm), greatest length of the skull shorter than 23mm (mean: 20.6mm), facial stripes present and inner upper incisor convergent at tips and widely separated at base (Díaz *et al.* 2016; Gardner 2008a; Goodwin 1958). Goodwin (1958), in *C. trinitatum* description, states that this species lacks dorsal stripe. However, a type's fetus had a conspicuous dorsal stripe. One of our specimens has a well-defined dorsal stripe. Even though our specimens lie within *C. trinitatum* characteristics, all measurements correspond to the lower range limit. Both genes were only obtained for one individual, JFD_01267 had only CYTB available. For both genes, sequences lie in a separate high supported monophyletic group (Fig 9A, B), with interspecific uncorrected p-distances of 5.35% for COI and 3.37% for CYTB with respect to the nearest group, *C. trinitatum.* This high genetic distance and the low intraspecific uncorrected p-distance (0.6%) within CYTB monophyletic clade plus de the tree topology presented herein suggest an undescribed cryptic diversity in *C. trinitatum* that needs further taxonomic assessment.
Molecular data remarks: The sequences reported here correspond to the first sequences for this haplogroup. Moreover, COI sequence forms a new BIN BOLD:ADZ8446.
Phylogenetic analysis: COI: 24, HKY+I+Γ, *Uroderma bilobatum*, 99.94%; CYTB: 14, HKY+I+Γ, *Uroderma bilobatum*, 96.97%.
Vouchers associated to sequenced material: JFD_01230; JFD_01267

Micronycteris megalotis
The genus *Micronycteris* includes 11 recognized species, some forming non monophyletic clades (Siles *et al.* 2013). *Micronycteris* is still lacking a complete taxonomic resolution, thus comprises some newly described species and other undescribed linages (Larsen *et al.* 2011; Porter *et al.* 2007; Siles *et al.* 2013). Five of these species are reported for Colombia (Ramírez-Chaves *et al.* 2016), although taxonomic clarity will probably reassess species occurrences and distribution. We captured one specimen belonging to the subgenus *Micronycteris* (Porter *et al.* 2007). This specimen was morphologically identified as *M. microtis*, as it has a small size, ears rounded and connected by an interauricular band of skin, fur on lower third of

medial edge of pinna 8 mm or shorter and dark ventral pelage (Díaz *et al.* 2016; Gardner 2008a). Nevertheless, sequence alignment place our sequence inside a well-supported monophyletic clade of *M. megalotis* (Fig 10B). Specifically, COI sequence lies within *M. megalotis* clade recognized by Clare et al. (2011), which includes all known sequences of *M. microtis.* Moreover, CYTB sequence clusters within Clade 3 of *M. megalotis* (Larsen *et al.* 2011; Siles *et al.* 2013) (Fig 10A). Clade 3 is more closely related with a clade composed by *M. buriri* and *M. megalotis* Clade 4, described in 2011 by Larsen et al. (2011). Our cluster (*M. megalotis* Clade 3) is genetically more similar to *M. megalotis* clade 4, with an uncorrected interspecif p-distance of 1.9%. Contrasting with the average Kimura 2-parameter distance obtain in Larsen et al. (2011) of 2.7% for these two clades. Our specimen differentiates morphologically from *M. buriri* in its weakly bilobed upper incisors, lobed and non-hypsodont lower incisors and deep basisphenoid pits with a complete septum that separates them (Larsen *et al.* 2011). These characteristics are more similar to specimens of *M. megalotis* of Venezuela and Trinidad and Tobago (Larsen *et al.* 2011). However, our specimen lacks the gap between M1 and M2 reported by Larsen et al. (2011) for a specimen of Clade 3 from Venezuela. In COI, *M. minuta* is *M. megalotis* sister species, with an uncorrected interspecific p-distance of 12.5%. Moreover, *megalotis* clade has a high genetic variation (i.e. uncorrected intraspecific p-distance of 4.2%). Even though a taxonomic revision in needed in order to improve *megalotis* identification, we named the sequences produced herein as *M. megalotis* Clade 3., representing an important additional point in its distribution.
Molecular data remarks: These are the first sequences from this species for Colombia. COI sequence clusters within BIN BOLD:AAA6107 assigned to *M. megalotis.*
Phylogenetic analysis: COI: 26, HKY+Γ, *Lampronycteris brachyotis*, 99.12%; CYTB: 40, HKY+I+Γ, *Lampronycteris brachyotis*, 99.12%.
Vouchers associated to sequenced material: JFD_01311

Phyllostomus hastatus.
The genus *Phyllostomus* has been stable, in terms of species number, for more than two decades. Van Den Bussche and Baker (1993) recognized *Phyllostomus* as a monophyletic clade comprising 5 species, including *Phylloderma stenops*. However, Gardner (2008a) and Rodríguez-Posada and Sánchez-Palomino (2009) place *Phylloderma stenops* in a different genus, leaving *Phyllostomus* with 4 species, all of them occurring in Colombia (Ramírez-Chaves *et al.* 2016; Rodríguez-Posada & Sánchez-Palomino 2009). This 4 species are readily identifiable by morphological characters (Gardner 2008a). We captured one specimen of *Phyllostomus* that had all characteristics of a *P. hastatus* (Díaz *et al.* 2016; Gardner 2008a). Molecularly, we were only able to obtain CYTB sequence. This sequence was aligned with the only two available sequences in NCBI for the genus (Velazco & Cadenillas 2011). Additionally, the alignment included all sequences reported in Van Den Bussche and Baker (1993). These last sequences are not uploaded to NCBI but represent the only source of information for all species in the genus, all having voucher specimens deposited in Texas Tech University. Each *Phyllostomus* species forms a well-supported monophyletic group except for *Phyllostomus hastatus* (Fig. 11). Our sequence is more closely related to *P. hastatus* group; however, they do not form a monophyletic group (Fig. 11). Uncorrected genetic p-distances within the paraphyletic group of *P. hastatus* is 3.23% and with its sister group, *P. elongatus* is 7.07%. As no COI sequences was generated, BIN analysis is unavailable. We proposed to call this sequence *P. hatatus* as its morphological traits correspond to this species and it is

more closely related to *P. hastatus* haplogroup. However, two subspecies are actually recognized within *P. hastatus*, separated by the Colombian Cordillera Oriental (Rodríguez-Posada & Sánchez-Palomino 2009). Our results invite for a broader taxonomic revision for this species as its not represented by a well-supported monophyletic group.
Molecular data remarks: Even though our sequence is not the first one for the species, it is the first for the western subspecies (*P. h. panamensis*).
Phylogenetic analysis: COI: no sequence data were recovered for this species; CYTB: 8, GTR+Γ, *Phylloderma stenops*, 67.1%, missing data is explained by the amplification of just 402 bp in Van Den Bussche and Baker (1993).
Vouchers associated to sequenced material: JFD_01222

Gardnerycteris crenulatum.
The genus *Gardnerycteris* comprises 3 species (Hurtado & D'Elía 2018). Just one species (*G. crenulatum*) is reported for Colombia (Hurtado & D'Elía 2018; Ramírez-Chaves *et al.* 2016) and *G. keenani*, a recently described species, possibly occurs within Colombian territory (Hurtado & D'Elía 2018). Our only specimen from this genus was identified using Gardner (2008a) and Díaz et al. (2016) as *G. crenulatum*. Moreover, a recent taxonomic study (Hurtado & D'Elía 2018) establishes species boundaries within the three species of the genus, both morphologically and molecularly. Using the diagnostic morphological traits proposed here, our specimens is more likely to be *G. crenulatum* as it has a witish dorsal stripe, noseleaf hairs evenly distributed around noseleaf, noseleaf rib hairs absent, complete noseleaf pigmentation, basioccipital narrow at cochlear level and basisphenoid pits shallow. However, other diagnostic characters are not present in our specimen and overlap with those of *G. keenani* (i.e. borders of pinnae not wrinkled, third metacarpal equal than fifth, anterior border of nasal bones not U-shaped and sagittal crest of the braincase low). Molecularly, COI and CYTB sequences were obtained for our specimen, both been first for Colombia. Both COI and CYTB alignments included all the terminals used by Hurtado and D'Elía (2018) and other taxa available in NCBI. CYTB phylogeny is in concordance with Hurtado and D'Elía (2018) as it represents each *Gardnerycteris* species by a well-supported monophyletic group. Our sequence clustering within *G. crenulatum* haplogroup (Fig 12A). This haplogroup is more closely related to *G. koepckeae* (6.5% uncorrected interspecific p-distance). Nonetheless, *G. crenulatum* has a high genetic variation, 5.4% uncorrected intraspecific p-distance. COI tree is also congruent with Hurtado and D'Elía (2018). This phylogeny, in spite of supporting *G. crenulatum* monophyly with high BS value (Fig 12B), does not supports the monophyly of *G. koepckeae* and *G. keenani.* All individuals of *G. koepckeae* (n=1) and one individual of *G. keenani* (n=3) are included within *G. crenulatum.* A different, well supported haplogroup comprising the other 2 specimens of *G. keenani* do form a monophyletic group which has an interspecific uncorrected p-distance of 12.8% with *crenulatum* group. Our sequences cluster within *G. crenulatum* haplogroup that has an uncorrected intraspecific p-distance of 2.8%. Moreover, our COI sequence clusters within the new BIN BOLD:AEA3129 of *G. crenulatum*. We named this sequence as *G. crenulatum* but suggest that a revision is made concerning species boundaries within this genus.
Molecular data remarks: Both CYTB and COI sequences are the first ones for Colombia. COI sequence forms a unique BIN BOLD:AEA3129.
Phylogenetic analysis: COI: 36, HKY+Γ, *Phyllostomus latifolius*, 98.9%; CYTB: 8, HKY+I, *Phyllostomus hastatus*, 89.7%.

Vouchers associated to sequenced material: JFD_01298

Lophostoma occidentalis.
Velazco and Cadenillas (2011), using morphological and molecular data, report 7 species within the genus *Lophostoma*. Additionally, in 2012 a white-ventered *Lophostoma* was described from Panama using only morphological data (Velazco & Gardner 2012). From the 8 recognized species of *Lophostoma*, 4 are reported for Colombia (Marin-Vasquez *et al.* 2014; Ramírez-Chaves *et al.* 2016). We captured 3 specimens that were morphologically identified as *L. occidentalis* as they don't have white venter, forearms are longer than 45mm (mean=55.3mm), p3 aligned with toothrow and indentation on the lingual cingulum of the upper canine weakly developed (Velazco & Gardner 2012). Molecularly, we were able to sequence 2 individuals for COI and 3 for CYTB. DNA alignment for CYTB was made using all sequences from Velazco and Cadenillas (2011) which include all sequences used in Baker et al. (2004). COI alignment was based on sequences produced by Clare et al. (2011). Published sequences for *L. occidentalis* were only available for CYTB, all of which form a well-supported monophyletic clade with the sequences produced in this study (Fig 13A). However, with high (3.9%) uncorrected intraspecific p-distance. Its more closely related species is *L. brasiliense* with an uncorrected p-distances of 7.5%. COI tree also supports the monophyly of *L. occidentalis* (Fig 13B), these 2 sequences differ from their closer relative (*L. silcicolum*) by an uncorrected p-distance of 9.6% and with each other, i.e. intraspecific uncorrected p-distance of 0.3%.
Molecular data remarks: Both COI and CYTB sequences are the first to be published. COI sequences cluster within the new public BIN BOLD:ADR4528.
Phylogenetic analysis: COI: 37, HKY+Γ, *Tonatia saurophila*, 98.7%; CYTB: 34, GTR+I, *Tonatia saurophila*, 98.4%.
Vouchers associated to sequenced material: JFD_01286; JFD_01291: JFD_1299

Uroderma covexum.
The genus *Uroderma* has been one of the most studied bat genera in the Neotropics (Mantilla-Meluk 2014). To date, five species are recognized (Mantilla-Meluk 2014), all occurring in Colombia except for *U. davisi* (Ramírez-Chaves *et al.* 2016). Morphologically, the four analyzed specimens belong to *U. convexum* as they have a conspicuous deflection of the nasal bones at the interorbital area, an arched (convex) upper tooth-row and the union of the nasal bones with respect to the maxillae forms an obtuse nasal angle in a lateral view (Díaz *et al.* 2016; Mantilla-Meluk 2014). Molecularly, both COI and CYTB sequences were obtained. COI alignment included at least one sequence of each clade in Clare et al. (2011). CYTB alignment was made with sequences from Hoffmann et al. (2003), giving special attention to include all chromosomal races identified by these authors, other available sequences were also included. Our CYTB tree is consistent with Hoffmann et al. (2003) as it represents all chromosomal races, who were later treated as valid species by Mantilla-Meluk (2014). Our sequences cluster with a marginal support value with chromosomal race 2N=38, i.e. *U. convexum* (Fig 14A). Not only this clade, but also all others in our phylogeny, have very low intraspecific uncorrected p-distance (mean=0.7%). Additionally, low interspecific uncorrected p-distance is also observed with its sister species, *U. bakeri,* a recently described species (Mantilla-Meluk 2014), with uncorrected interspecific p-distance of 1.4%. COI tree shows similar results, besides a low intraspecific uncorrected p-distance of 1%, our sequences cluster with low support value with individuals probably misidentified as *U. bilobatum* (Fig 14B), but who represent *U.*

convexum monophyletic group. This group also presents a low interspecific uncorrected p-distance with its sister group *U. bilobatum* (i.e. 1.8%). Clare et al. (2011) recognized two clades of *U. bilobatum* one of them been the *U. convexum* clade reported here. Moreover, all our COI sequences cluster within BIN BOLD:AAA2524 that needs to be renamed as *U. convexum.* In spite of *Uroderma* been among Neotropical bats, one of the most intensively studied genera, including studies of multiple datasets documenting its karyotypic, molecular, and morphological variation (Mantilla-Meluk 2014), no Colombian sequences had been published until this study. Our sequences represent a key point for the understanding of geographical DNA variation among *Uroderma* taxa.
Molecular data remarks: Both COI and CYTB sequences are new to Colombia. COI sequences cluster within BIN BOLD:AAA2524.
Phylogenetic analysis: COI: 36, HKY+Γ, *Platyrrhinus helleri*, 99.4%; CYTB: 64, HKY+Γ, *Platyrrhinus helleri*, 99.9%.
Vouchers associated to sequenced material: JFD_1219; JFD_01240; JFD_1285; JFD_1302

Platyrrhinus helleri.
Platyrrhinus is one of the most speciose genera in the family Phyllostomidae, with 21 species currently recognized (Velazco & Lim 2014). More than half of this diversity, 14 species, occurs in Colombia (Ramírez-Chaves *et al.* 2016). Morphological traits to recognize all species in the genus have been widely discuss (Velazco 2005; Velazco *et al.* 2010; Velazco & Lim 2014; Velazco & Patterson 2008). Here we characterized 4 specimens as *P. helleri* following the diagnostic characters in Velazco and Patterson (2008). Except for a badly prepared specimen, where neither the interramal vibrissae nor the 7 vibrissae around noseleaf were possible to detect, all specimens possess all characteristics of a *P. helleri.* We obtained COI and CYTB sequences for all four specimens. In terms of CYTB, sequences have been sparsely produced for almost all species (i.e. 18) in the genus (Velazco *et al.* 2010; Velazco & Lim 2014; Velazco & Patterson 2008), thus our alignment includes at least one sequence for each species. Our sequences cluster within the well supported monophyletic group of *P. helleri* (Fig 15A). This clade is more closely related to *P. matapalensis* (uncorrected interspecific p-distance of 2.7%). Most species in the genus form well supported monophyletic groups, showing little intraspecific divergence (mean uncorrected p-distance of 0.5%). COI tree resembles that of Clare et al. (2011), as it includes all 7 species that have been sequenced for COI. Our sequences cluster within *P. helleri* monophyletic group (Fig 15B). This clade was not only recognized by Clare et al. (2011) (i.e. comprising 4 independent lineages), but also has a high uncorrected intraspecific distance (i.e. 3.2%). Additionally, this sequences cluster within BIN BOLD:AAA2242.
Molecular data remarks: Both sequences (COI and CYTB) are the first ones produced in Colombia for this species.
Phylogenetic analysis: COI: 35, HKY+Γ, *Vampyrodes caraccioli*, 98.7%; CYTB: 74, HKY+Γ, *Vampyrodes caraccioli*, 99.5%.
Vouchers associated to sequenced material: JFD_01218; JFD_01243; JFD_01268; JFD_01278

Vampyressa thyone.
The genus Vampyressa comprises 5 neotropical species (Hernández-Canchola *et al.* 2019), two of them, *V. sinchi* and *V. elisabethae*, recently described using just morphological data (Tavares *et al.* 2014). Three out of the five species are distributed

in Colombia (Ramírez-Chaves *et al.* 2016). Our two specimens were identified as *V. thyone*. Their measurements fit to those reported in Tavares et al. (2014) morphological revision. However, they differ in the shape of the mesopterygoid fossa, since Díaz et al. (2016) state that *V. thyone* has a narrow ("V" shape) mesopterygoid fossa, but our two specimens present a "U" shaped fossa, which is a character observed in the larger species of Vampyressa (e.g. *V. melissa*). COI and CYTB alignments were constructed with all available sequences for Vampyressa, including 2 and 3 species respectively. The topology of our ML phylogeny is similar to previous phylogenies (Hernández-Canchola *et al.* 2019; Hoofer & Baker 2006; Porter & Baker 2004; Velazco & Patterson 2008) reported for the species. Both COI and CYTB sequences cluster within a monophyletic group of *V. thyone* (Fig 16B, A respectively), CYTB with a high support value. Both analyses support *V. thyone* as sister group of *V. pusilla*, CYTB with 9% of uncorrected net p-distance and COI with 10%. Moreover, and as reported by Hernández-Canchola et al. (2019), using CYTB, we also detected three geographic clades within *V. thyon*e (Fig 16B). A first clade from Peru to Panama, another from Costa Rica to Honduras, and a third lineage from Mexico. Our two sequences grouped with the lineage from Peru to Panama. Hernández-Canchola et al. (2019) recommend a taxonomic revision to validate the taxonomic status of the three groups, nevertheless the uncorrected p-distance within all the *V. thyone* is just of 1.7% (CYTB) and 0.7% (COI). These numbers fall far below the 5% value commonly regarded as a hallmark of species-level divergence (Baker & Bradley 2006a). Additionally, this sequences cluster within the same BIN BOLD:AAA6871.
Molecular data remarks: Both sequences (COI and CYTB) are the first ones produced in Colombia.
Phylogenetic analysis: COI: 10, HKY+I, *Mesophylla macconnelli*, 99,78%; CYTB: 19, HKY+I, *Mesophylla macconnelli*, 96,74%.
Vouchers associated to sequenced material: JFD_01287; JFD_01292

Carollia
Despite being one of the most common bats in the New World scientific collections, the genus *Carollia* presents a confusing taxonomy, resulting in a constant variation in the number of species (Baker & Bradley 2006b; Velazco 2013; Zurc & Velazco 2010). In the last decades, several undescribed species were recognized from populations usually assigned to other *Carollia* species (Solari & Baker 2006). Also, some species were reassigned as junior synonyms (Baker *et al.* 1994b; Zurc & Velazco 2010), and there is still cryptic diversity in the *C. castanea* and *C. brevicauda* group that needs morphological and molecular revision (Baker & Bradley 2006b; Solari & Baker 2006; Velazco 2013). Here we will follow Velazco (2013) species number, where he lists eight species for the genus, four of which are distributed in Colombia (Zurc & Velazco 2010) plus one species to be described (Ramírez-Chaves *et al.* 2016). We captured 16 specimens that were morphologically identified as *Carollia castanea* (5) and *Carollia brevicauda* (11).

Carollia casatanea
Historically, *Carollia castanea* has been easily identified due to its small size, compared with other species within the genus, that don't overlap in most of the measures used as diagnostic characters (basilar length [15.52 ± 0.97], maxillary toothrow length [6.2 ± 0.40], ventral rostral length [5.13 ± 0.39], coronoid-angular distance [4.3 ± 0.45], mandibular length [12.3 ± 0.75], and coronoid height [3.8 ± 0.55]) (McLellan 1984; Muñoz *et al.* 2004; Zurc & Velazco 2010). Three of our specimens fit

within the aforementioned range of measurements described for *C. castanea* (basilar length [mean: 14.93mm], maxillary toothrow length [mean: 6.06mm], ventral rostral length [mean: 5.2mm], coronoid-angular distance [mean: 4.1mm], mandibular length [mean: 11.79mm], and coronoid height [mean: 3.8mm]). However, and contrary to the characters listed in Gardner (2008b) and Díaz et al. (2016) our specimens differ from *C. castanea* since: 1) they present a color pattern of dorsal pelage with alternating and contrasting dark, pale and dark brown bands, differing with the indistinct banding pattern reported in Díaz et al. (2016), 2) in some specimens the second upper premolar and the first upper molar aren't in contact showing an evident gap, character not expected for *C. castanea* and 3) the mesopterygoid fossa shape is variable, we observed U-shaped (specific to *C. brevicauda* and *C. persipicillata*) and V-shaped (specific *C. monohernandenzi* and *C. castanea*) fosses in ours specimens. The ML analysis using CYTB recovered a similar topology as reported in the literature (Solari & Baker 2006; Velazco 2013), where two major clades can be distinguished. One including the smaller species (i.e., *C. benkeithi, C. castanea and C.* sp.), while the other containing the medium to large species (*C. subrufa, C. sowelli, C. brevicauda, C. perspicillata, C. manu*). Our sequence forms a well-supported (100 BS) monophyletic group with other sequences of *C. castanea* from Panama (Fig 17), being our sequences, the first ones reported from Colombia. Nonetheless, and as also reported previously (Baker & Bradley 2006b; Velazco 2013), *C. castanea* was found to contain two haplogroups, with an intraspecific uncorrected p-distance of 2.6%. Even when this distance is within the accepted rage for specimens of the same species (Bradley & Baker 2001), it is not only the greatest among all monophyletic groups in our analysis, but also has an interspecific uncorrected p-distance between castanea haplogroups of 3.2%. This value was greater than the uncorrected p-distance observed between other sister species in our analysis (i.e. perspicillata-brevicauda, 2.6%; perspicillata-sowelli, 2.9%) and was far greater that the intraspecific distance of each of the *C. castanea* haplogroups (*C. castanea* A: 1.3% and *C. castanea* B: 0.23%). Since there isn't sufficient information to assign to which of the two lineages the name C. *castanea* should be applied to, we followed Velazco (2013) and named the haplogroups as *C. castanea* A and *C. castanea* B (Fig 17), being the last one the haplogroup of Colombian and Panamanian specimens. As done by other authors (Baker & Bradley 2006b; Velazco 2013), we suggest further studies to distinguish clades A and B, and assign to one of them *C. castanea sensu stricto.*

Molecular data remarks: CYTB sequences are the first ones for this species in Colombia.

Phylogenetic analysis: COI: no sequence data was recovered for this species; CYTB: 133, HKY+I+Γ, Rhinophylla fischerae, 97,47%.

Vouchers associated to sequenced material: JFD_01281; JFD_1301; JFD_01300

Carollia perspicillata

C. perspicillata is the largest species within the genus *Carollia* (Díaz *et al.* 2016; McLellan 1984). Eight of our specimens were identified as this species following the measurements reported in McLellan(1984), Muñoz et al. (2004), and Zurc and Velazco (2010). However, regarding qualitative characters, our specimens not only present high morphological variation, but also combine characters of different species and even characters not yet described in the literature. First, Zurc and Velazco (2010) used a U-shaped mesopterygoid fossa as a diagnostic character to identify *C. perpicillata*. However, our specimens show variation in this character. Just two of them present a U-shaped fossa (JFD_01224, JFD_01274), other two show a V-shaped one

(JFD_01221, JFD_01250) which is a diagnostic character to identify *C. castanea* and *C. monohernandezi*, and the remaining four (JFD_01229, JFD_01234, JFD_01275, JFD_01319) feature a W-shaped mesopterygoid fossa, a character state that hasn't been reported previously for any species within the genus. Second, Díaz et al. (2016) state an indistinct dorsal pelage banding pattern, however, our specimens present a dorsal pelage color pattern with alternating dark, pale and dark bands. Also, our specimens' maxillary toothrow is divergent posteriorly, contrasting the straight line of superior teeth reported. Third, Gardner (2008b) state that the hair on nape of neck is shorter, with less indistinct basal bands, but our specimens showed the same color pattern and hair length along the dorsal pelage. Lastly, the shape of the posterior margin of uropatagium is a relevant diagnostic character to identify *Carollia* species (Velazco 2013; Zurc & Velazco 2010). *C. perspicillata* is expected to have a V-shaped uropatagium. Our specimens showed variation in this character, but no relevance was given to this variation because it may be due to the specimen preparation. For the molecular analysis, our COI sequence clusters within BIN BOLD:AAA0002 formed by *C. perspicillata* sequences. Regarding the ML analysis, the tree obtained using COI wasn't informative, since no monophyletic groups, except by *C. castanea* and *C. sowelli*, were formed (data not shown). Our specimens are part of a paraphyletic group of *C. perspicillata*. About CYTB analysis, our specimens lie within a marginally supported (62% BS) monophyletic group with all other sequences of *C. perspicillata* (intraspecific p-distance of 1.6%) within the major clade of larger *Carollia* species (Fig 17). Its more closely related species is *C. brevicauda* with an uncorrected p-distances of 2.6%. This interspecific distance is below the 5% value used for application of the Genetic Species Concept suggesting that *C. perspicillata* and *C. brevicauda* could be the same species. Nevertheless, and even though *C. brevicauda* and *C. perspicillata* are sympatric, these 2 species do not hybridize (Pine 1972). Moreover, both species are readily identifiable by morphological means (Ruelas 2017) even though, and as confirmed herein low intra- and inter- specific genetic distances have been frequently reported (Baker & Bradley 2006b; Velazco 2013). Therefore, it would be inappropriate to include *C. brevicauda* and *C. perspicillata* in a single species (Baker & Bradley 2006b).

Molecular data remarks: The *C. perspicillata* sequences generated here are the first ones for Colombia. COI sequences cluster within BIN BOLD:AAA0002 assigned to *C. perspicillata*.

Phylogenetic analysis: COI: 137, HKY+I+Γ, *Rhinophylla alethina*, 98,77%; CYTB: 133, HKY+I+Γ, *Rhinophylla fischerae*, 97,47%.

Vouchers associated to sequenced material: JFD_01221; JFD_01224; JFD_01229; JFD_01234; JFD_01250; JFD_01274; JFD_01275; JFD_01319

Artibeus-Dermanura

Although the Fruit-eating bats, *Artibeus*, comprise the most speciose genus in the family Phyllostomidae and one of the most common groups of bats in Neotropical lowland forest (Larsen *et al.* 2010; Lim *et al.* 2008), resolution of taxonomy and their identification has been difficult, especially because there isn't consensus about the taxonomy status of *Artibeus, Dermanura* and *Koopmania* (Hoofer *et al.* 2008; Larsen *et al.* 2010). Some authors argue that *Artibeus* and *Dermanura* could be diagnosed as separated genera on the basis of morphology (Smith 1976; Solari *et al.* 2007, 2009), karyology (Baker 1973) and restriction sites data (Van Den Bussche *et al.* 1993). However, the recognition of these two genera is not widely accepted, and in most publications *Dermanura* is considered a subgenus of *Artibeus* (Hoofer *et al.* 2008;

Redondo *et al.* 2008; Simmons 2005). Following Lim et al. (2004) and Wetterer et al. (2000) we treat *Dermanura* (the small *Artibeus*) as a subgenus of *Artibeus*. This genus encompasses at least 23 nominal species (11 *Dermanura* and 12 *Artibeus* including *Artibeus koopmania concolor*) from which 14 are distributed in Colombia (Ramírez-Chaves *et al.* 2016). Three species, *Artibeus lituratus, Artibeus planirrostris* and *Artibeus* (*dermanura) anderseni* were characterized (15 specimens) in this study. Both COI and CYTB genes were sequenced for at least two specimens of each species. COI alignment included 17 species, while CYTB alignment represented almost all species except for *A. equatorialis*.

Artibeus (*Dermanura) anderseni*

Four specimens of *A. d. anderseni* were captured and sequenced, generating the first sequences of the species for Colombia. With both genes, COI and CYTB, our sequences form, with all other sequences reported for *A. d. anderseni*, a well-supported monophyletic group with 80 and 96% BS value, respectively (Fig 18A, B). Also, all sequences were grouped within the same new BIN BOLD:ADZ9406. With COI, *A. d. anderseni* shows an intraspecific uncorrected p-distance of 1.3% and with *A. d. cinereus,* its closest related group, an interspecific uncorrected p-distance of 2.8%. Regarding CYTB, the intraspecific uncorrected p-distance is 1.2% and the interspecific uncorrected p-distance, with *A. d. rava*, is 5.7%. Molecularly, our specimens certainly seem to be *A. d. anderseni*, nonetheless, their morphological traits are not in concordance with those proposed as diagnostics characters (Díaz *et al.* 2016; Gardner 2008b). Osgood (1916) who described for the first time *A. d. anderseni,* stated that it was a small species, with a forearm length ranging from 34 to 36mm, without evident light facial stripes and with a first upper molar reduced in height compared with the second one. Our specimens show evident white facial stripes, the first upper and second molar have the same height and the forearm length was greater than 37mm (mean= 37.15). Moreover, using Gardner (2008b) and Díaz et al. (2016)'s keys we weren't able to reach a nominal taxon. Firstly, because these two keys don't match in the diagnostic character used to differentiated *A. d. anderseni* from the other species of the genus. Secondly, because in some cases our specimens fit characters in both dichotomic options. For example, in Garner et al. (2008b) *A. d. anderseni* is expected to have an uropatagium thinly haired, the rostrum is usually elevated anteriorly and the maxillary toothrow is nearly parallel. Our specimens definitively fit the first character but regarding the direction of the toothrow, it is convergent anteriorly and the rostrum isn't elevated, which are characters of *A. d. phaeotis,* the respective dichotomic option in the key (interfemoral membrane thickly haired, maxillary toothrow convergent anteriorly and rostrum usually not elevated anteriorly). Therefore, and rather than suggesting cryptic diversity within *anderseni* due to the aforementioned morphological disparities, we propose, based on the low intraspecific uncorrected p-distance reported herein, a thorough revision of the species including historically forgotten Colombian morphological variation.

Molecular data remarks: Both COI and CYTB sequences are the first ones for this species in Colombia. Moreover, COI sequences represent a unique BIN BOLD:ADZ9406.

Phylogenetic analysis: COI: 298, GTR+I+Γ, *Enchistenes hartii*, 97.83%; CYTB: 379, HKY+I+Γ, *Enchistenes hartii*, 99.13%.

Vouchers associated to sequenced material: JFD_01228; JFD_01247; JFD_01276; JFD_01284; JFD_01303

Artibeus lituratus

Two specimens of larger *Artibeus* were captured but until molecular data was available, we weren't able to identify them as any species. Not only because they don't fit any dichotomous keys (Díaz *et al.* 2016; Gardner 2008b; Haynes & Lee 2004), but also because these two specimens differ morphologically. They differ mainly in the shape and number of teeth. The specimen JFD_01279's first upper incisors are less than twice the size of the second, resemble them in shape; and are in contact with each other. In the other hand, the upper incisors of the specimen JFD_01280 differ in shape and have an evident gap. Haynes & Lee (2004) and Gardner (2008b) state that in *A. lituratus* the third lower molar is absent and the hypocone of the first upper molar is not well developed, none of our specimens fulfill this pattern. JFD_01279 does not have m3 but the hypocone of the M1 is well developed compared with other specimens of the genus. Contrastingly, JFD_01280 fits the hypocone character but presents m3. This last pattern, the combination of m3 and hypocone of M1 poorly developed are diagnostic characters used in Gardner (2008b) to identify *A. planirostris*. However, our specimens are not *planirostris* because both JFD_01279 and JFD_01280 are below the minimum accepted length of skull (29.5 mm) and breadth across upper molars (14 mm) (Lim 1997). Moreover, our specimens present evident facial stripes and red brownish fur, diagnostic characters of *A. lituratus* (Haynes & Lee 2004). In spite of the high morphological variation presented here, both specimens were grouped with all other sequences reported for *A. lituratus*. In the CYTB analysis our sequences lie within a well-supported monophyletic group (intraspecific uncorrected p-distance of 1%) (Fig 18A) while in the COI analysis they from a poorly supported one (Fig 18B) (intraspecific uncorrected p-distance of 0.87%). In both trees a group composed by *A. plinorostirs* and *A. amplus* (plus A. obscurus in COI) were the closest group with interspecific uncorrected p-distances of 4.7% in CYTB and 1.6% in COI. Additionally, COI sequences founded the BIN BOLD:AAA0874, grouping only sequences of *A. lituratus*. As concluded above with *D. anderseni,* we do not think the the aforementioned morphological variation is showing cryptic diversity, but it is showing that morphological variation of Colombian specimens has not been taken into account in the species description and key design. That's why we named those specimens as *A. lituratus* and suggest a morphological revision.

Molecular data remarks: The sequences obtained here are the first ones reported for Colombia. COI sequences cluster within BIN BOLD:AAA0874 assigned to *Artibeus lituratus*.

Phylogenetic analysis: COI: 298, GTR+I+Γ, Enchistenes hartii, 97.83%; CYTB: 379, HKY+I+Γ, Enchistenes hartii, 99.13%.

Vouchers associated to sequenced material: JFD_01279; JFD_01280

Artibeus planirostris

Following Lim (1997) and Hollis (2005) we identify seven specimens as *A. planirrostris*. In concordance with the species description, our specimens possess M3 and have faint, but always present, facial stripes (Hollis 2005). However, regarding diagnostic character based on size (palatal length, maxillary toothrow length, zygomatic breadth, interorbital width, rostral length, width across upper canines, coronoid height), all but one (JFD_01255) of our specimens are in the overlapping region with *A. jamaisensis*. Actually, for the cranial length and width across upper canines measurements our specimens fall within the *A. jamaisensis*' range (Lim 1997). However, molecularly they were identified as *A. planirostris*. ML analysis using CYTB, generated a well-supported monophyletic group with all other *A. planirostris* sequences (Fig 18A), with an

intraspecific uncorrected p-distances of 1.6%. Contrastingly, the well-supported monophyletic group of *A. planirostirs* recovered in COI (Fig 18B), was poorly supported and presented an intraspecific uncorrected p-distances of 0.8%. In both trees *A. amplus* is the closest group with an interspecific uncorrected p-distances of 2.6% with CYTB and 1.5% with COI. All seven COI sequences form a new BIN BOLD:ABZ9500.
Molecular data remarks: Both COI and CYTb are the first reported sequences for Colombia.
Phylogenetic analysis: COI: 298, GTR+I+Γ, Enchistenes hartii, 97.83%; CYTB: 379, HKY+I+Γ, Enchistenes hartii, 99.13%.
Vouchers associated to sequenced material: JFD_01246; JFD_01252; JFD_01254; JFD_01255; JFD_01266; JFD_01272; JFD_01273

Vespertilionidae.

Myotis sp.
Occurring worldwide and with about 100 known species, *Myotis* is a widely distributed and specious genus (Gardner 2008a). The most recent review, focused on American *Myotis*, report 42 New World species, i.e. 26 in North America, 11 in Central America, 15 in South America and 5 in the Caribbean (Larsen *et al.* 2012), 10 of them occurring in Colombia (Ramírez-Chaves *et al.* 2016). Nevertheless, and after analyzing a big dataset, Larsen et al. (2012) concluded that is it likely that the number of Neotropical *Myotis* is underestimated. In fact, several new species of South American *Myotis* have been recently described (Haynie *et al.* 2016; e.g. Moratelli *et al.* 2013; Moratelli & Wilson 2014). Haynie et al. (2016) description showed that even two sister species with high morphological disparities could have little genetic differentiation. Species of *Myotis* have been difficult to identify and no clear morphological boundaries exist between species, especially in widely distributed taxa as *M. nigricans* (Larsen *et al.* 2012). Therefore, many of the species represent paraphyletic clades (Haynie *et al.* 2016; Larsen *et al.* 2012). Morphologically, three of our four specimens possess all characteristics of *M. nigricans* and one possess all characteristics of *M. caucencis*. The only difference is forearm length (Díaz *et al.* 2016; Moratelli *et al.* 2013), three of them under and one of them above 36mm, *M. nigricans* should have a forearm less than 36mm and *M. caucencis* more than 36mm. For all 4 specimens we were able to obtain COI and CYTB sequences. COI alignment includes all clades found in Clare et al. (2011), while CYTB alignment used all not replicated sequences from Larsen et al. (2012) and from Haynie et al. (2016). Even though, all our sequences form an independent-well supported monophyletic clade with intraspecific uncorrected p-distances of 0%, both (COI and CYTB clusters) have different sister groups (Fig 19B, A respectively). In the first place, COI sequences have as sister group two undescribed species of *M. riparius* (i.e. *M. riparius* S1 and *M. riparius* S2) from Guyana recognized by Clare et al. (2011). Our sequences cluster has an uncorrected interspecific p-distance of 3.1% with its sister cluster (i.e. *M. riparius* S1 and *M. riparius* S2). Alternatively, CYTB is more closely related with a specimen identified by Larsen et al. (2012) as *Myotis* cf. *keaysi* haplogroup 1. This sequence has an uncorrected interspecific p-distance of 4.57% with our cluster. Additionally, all our COI sequences cluster within a new BIN BOLD:AEA0898. Considering that 1) morphologically our specimens show clear differences with both sister species (i.e. no sagittal crest, uropatagium and plagiopatagium completely naked and no fringe in uropatagium), 2) genetic distance values as low as 2.0% separate currently recognized species of

Myotis (Larsen *et al.* 2012) and 3) tree topology shows clear phylogenetic differentiation, these evidence could represent an unrecognized species of *Myotis*. As such we could not give a name to this haplogroup, leaving it as *Myotis sp.* Our results support the hypothesis that South American *Myotis* diversity is underestimated due to the lack of research and collection (Larsen *et al.* 2012).
Molecular data remarks: These sequences are not only the first published sequences for both COI and CYTB for this haplogroup, but are the first ones for all the genus in Colombia. COI sequences form a new BIN BOLD:AEA0898.
Phylogenetic analysis: COI: 50, HKY+I, *Myotis brandtii* (Old World *Myotis*), 99.92%; CYTB: 125, HKY+I+Γ, *Kerivoula papillosa*, 98.85%.
Vouchers associated to sequenced material: JFD_01308; JFD_01309; JFD_01310; JFD_01312.

Rodentia.

Notosciurus granatensis
The genus *Notosciurus* comprises 2 nominal species (Gardner 2008b), with no consensus about subgenus and subspecies number (Gardner 2008b; Thorington *et al.* 2012). Both species, *N. granatensis* and *N. pucheranii* are widely distributed in Colombia (Ramírez-Chaves *et al.* 2016). Our only specimen was unequivocally identified as *N. granatensis* following morphological traits reported in Nitikman (1985) and Gardner (2008b). No ML analysis was performed using COI since our sequences is the first reported for the genus, and the one that founded the BIN BOLD:ADZ8687. Regarding CYTB, our sequence forms a monophyletic group with the only two other sequences (Panamá: HG962398, Costa Rica: KC758866) of the genus (Fig 20), with an intraspecific uncorrected p-distance of 1.4%.
Molecular data remarks: Both COI and CYTB are new for Colombia. COI sequences forms a new BIN BOLD:ADZ8687.
Phylogenetic analysis: COI: no tree was generated; CYTB: 3, HKY+I+G, *Sciurus variegatoides*, 92.31%.
Vouchers associated to sequenced material: JFD_01307

Proechimys semispinosus
Proechimys is the most speciose and geographically most widely distributed genus of the family Echimyidae. At least 22 species of *Proechimys* are recognized (Gardner 2008b; Steiner *et al.* 2000), with 9 species distributed in Colombia (Ramírez-Chaves *et al.* 2016). However, several authors (Gardner 2008b; Pine *et al.* 1981; Steiner *et al.* 2000) recognized that this number underestimates the actual number of species in the genus as *Proechimys* remains what may be one of the most problematical mammal genera taxonomically. We identify our 7 specimens as *P. semispinosus* (species group) using Gardner and Emmons (1984), Aguilera and Corti (1994), Carvalho and Salles (2004) and Gardner (2008b). However, in the juvenile specimen JFD_01297 we observed some variation in the pelage color and total and tail length. However this specimen filled all the other diagnostic characters and since, not only age-related changes but also polymorphism of external characters due to geographic and non-geographic variation has been reported for the genus (Gardner 2008b; Lara *et al.* 1992; Patton & Rogers 1982) we still named it as *P. semispinosus* (species group). Both COI and CYTB sequences were produced for all individuals, being the first sequences for Colombia. Regarding ML, COI tree includes other sequences of *P. semispinosus* but our sequences don't group with them or with any other species (Fig

21B). They form a monophyletic group with an intraspecific uncorrected p-distance of 0.14% and an interspecific uncorrected p-distance with published records of *P. semispinosus* of 6.3%. Moreover, this one isn't the lowest distance, with *P. longicaudatus* and *P. brevicauda* our sequences have an uncorrected p-distance of 4.8% and 6.1%, respectively. And its sister group in the topology is *P. quadruplicatus* with whom has an uncorrected p-distance of 11.7%. Similarly, in CYTB analysis our sequences form a monophyletic group (Fig 21A) (intraspecific uncorrected p-distance 0.13%). But in this case, *P. semispinosus* NCBI's sequences formed the closest related group with an interspecific uncorrected p-distance of 6.9%. Moreover, COI sequence is the first public sequence in the BIN BOLD:ADR6889 of *P. semispinosus.* Since there isn't clarity about the number and distribution of the species, current morphological characters are not sufficient for identifying *proechimys* specimens, and very few systematic studies have been performed, and even when our specimens don't group molecularly with what has been reported as *P. semispinosus* we named them as *P. semispinosus* (species group) (Gardner 2008b) and suggest a throughout morphological revision, not only for the *semispinosus* group but for the whole genus.
Molecular data remarks: Both COI and CYTB sequences are new to Colombia, COI sequences is the first public sequence for the BIN BIN:BOLD:ADR6889.
Phylogenetic analysis: COI: 82, HKY+I+Γ, *Echimys chrysurusas*, 99.94%; CYTB: 111, HKY+I+Γ, *Hoplomys gymnurusas*, 99.15%.
Vouchers associated to sequenced material: JFD_01235; JFD_01236; JFD_01271; JFD_01297; JFD_01306; JFD_01320; JFD_01321

Discussion.

Not surprisingly, the Neotropical region mirrors the DNA Barcoding trend of the world, with the largest proportion of DNA barcoding conducted for arthropods (Fig. 2A) (Taylor & Harris 2012). This, as stated by Taylor and Harris (2012) may be due to the poor taxonomic knowledge within this diverse group, especially when dealing with larval stages. The opposite side of this trend can be seen in clade such as birds, mammals and amphibians, which represent the minority of the produced sequences (Taylor & Harris 2012). Conversely, fish do not seem to follow such global trend. Here we report that this group represents just 3.4% from Neotropical barcodes (Fig. 2A), contrasting with 10% in the world (Taylor & Harris 2012). More regionally, taxa representation in Colombia differs slightly from comparable countries like South Africa, both harboring more than one biodiversity hotspot (Zachos & Habel 2011). Even though insects are still the most barcoded clade, followed by fish (da Silva & Willows-Munro 2016), Colombia has done considerable work in amphibians. Although, as South Africa we have also relegated the advance in groups as mammals and birds (Fig. 2B) (da Silva & Willows-Munro 2016).

Most barcoding efforts have been implemented by researchers from developed countries, even when most of Earth's biodiversity is found elsewhere (Vernooy *et al.* 2010). For instance, Canadian institutions have done intense fieldwork in the Neotropics and have also produced most of the available DNA barcodes for Neotropical small mammals (Borisenko *et al.* 2008; Clare 2011; Clare *et al.* 2007, 2011; Lim 2017). This effort was mainly done through collaborative work between BOLD and the Royal Ontario Museum (ROM) (Lim 2012). Resulting, as recognized by Lim (2012) in strong sampling bias in terms of geographic coverage (Fig. 2D). By 2012

most Andean mammals had not been barcoded, with complete absence of records from Colombia, Peru, Bolivia, Chile and Argentina (Lim 2012). Although some barcoding advances have been done in these countries (Fig. 2D), mammalian biodiversity is still poorly represented. In fact—considering each BIN as a different species—only 1.4% of all known mammalian species for Colombia have been barcoded (7 BINs out of 518 species mammal species—Ramírez-Chaves *et al.* 2016). Whereas, other well sampled countries like Mexico, Guyana and Suriname have barcoded, respectively 82.7, 68.4 and 44% of their diversity (total species numbers from Lim *et al.* 2005 and Ramirez-Pulido *et al.* 2014).

The underrepresentation of South American mammals in COI reference databases, is not only problematic for species identification, discovery and delimitation, but other tools from, or related to barcoding are also questionable. First, suggested intra- and inter-specific sequence divergence thresholds (Hebert *et al.* 2003a; b; Hebert & Gregory 2005) have been criticized as they may i) vary among taxonomic groups, ii) not be in agreement with taxonomic knowledge, or iii) may just not exist (i.e. overlap between intra- and inter-specific pairwise genetic distances) (Meyer & Paulay 2005; Reeder *et al.* 2007; Wiemers & Fiedler 2007). As summarized by Reeder et al. (2007) "a certain distance value in a single gene will not always resolve the presence or absence of 2 species". Second, Kimura 2 parameters (K2P) has been used as *de facto* DNA evolution model to estimate sequence divergence and tree topology (Collins *et al.* 2012). Although Collins *et al.* (2012) found that identification rates were not affected by model selection, the use of K2P may hinder the results of phylogenetic analyses (Srivathsan & Meier 2012). Third, South America's mammalian cryptic diversity may not be completely recovered by a single gene approach, especially when other lines of information are missing (e.g. morphological, ecological) (Clare *et al.* 2011).

Colombian case is even more special as most of its mammalian fauna is not included in systematic revisions. Therefore, local phenotypic diversity is not taken into account in dichotomous keys or species diagnosis, resulting descriptions that do not fully encompass all the morphological variants of a species. In this context, DNA barcoding in undersampled (molecularly and morphologically) countries operates poorly, as sequences are frequently associated to misidentified identified vouchers. Therefore, simple COI barcoding is not sufficient to describe most Neotropical biotic diversity. Here we present the first integrative contribution to barcoding mammals in Colombia. As we used diverse methodologies, our results—although limited in their geographic reach—are a great contribution to the taxonomy of small mammals in Northern South America. As an example, we sequenced for the first time in Colombia 25 species, more than four times the species currently available in BOLD for the country.

These sequences are not just valuable because of the sequence itself, but also due to the meticulous taxonomic effort employed that resulted in novel findings. For instance, we present cases where despite morphological disparities between our specimens and their diagnosis, they were recovered as strongly supported clades with haplotypes of that species (e.g. *Artibeus lituratus, Dermanura anderseni, Molossus rufus, Vampyressa thyone*). Conversely, some other specimens do not follow any diagnosis, nor they cluster with any available sequences of their genus (this represents "clades" where a thorough taxonomic revision is needed and where undescribed diversity may be present, *Chiroderma sp.*, *Molossus sp., Myotis sp.*). We also present instances with high concordance between morphological and molecular methods (e.g.

Didelphis marsupialis, *Caluromys lanatus*). Contrastingly, we found cases in which morphological identification agrees with literature (species description and dichotomous keys), however sequences cluster with a high intraspecific genetic p-distance with other sequences of the species (e.g. *Proechimys semispinosus*). Lastly, cases with accurate morphological concordance but high genetic distance were also found (e.g. *Desmodus rotundus*, *Phyllostomus hastatus*, *Lophostoma occidentalis*). Altogether, we found evidence of large variation in COI and CYTB intra- and inter-specific distances between different species and genera. These findings—although contrary to some authors (Baker & Bradley 2006a; e.g. Hebert *et al.* 2003b)—are in concordance to what has been concluded for some Neotropical mammals where fixed genetic distance thresholds do not provide a universal threshold for differentiating two species (e.g. mammals Clare 2011).

The results presented herein would have not been possible using DNA barcoding as it is traditionally proposed, i.e. a single gene identification technique (Hebert *et al.* 2003a). In fact, we observed that a sole source of information (morphology, phylogeny or distance-based methods), is not sufficient to accurately identify taxa. Here we deal with all the aforementioned barcoding problems and show the need for an integrative approach when constructing a barcoding reference database for highly diverse Neotropical clades.

Conclusions.

This project, although small in its geographic range, is an great contribution to the taxonomy of small mammals in Northern South America, one of the most biodiverse, yet least studied regions. Even though Colombia has a National Strategy for DNA barcoding, aiming 1 million records in BOLD by 2030 (CONPES-3934 2018) if this effort is not well conducted we will produce non informative barcodes that will just inflate our statistics but will not be useful in a more applied way (e.g. illegal traffic assessment, roadkill fauna). Here we present the first case of informative, careful-produced barcodes for mammals, an invitation to good barcoding practices for Colombian mammals. In addition to producing new barcodes for Colombia and the World, we present relevant taxonomic annotations for some Neotropical mammals. Those species need a thorough taxonomic revision, not only because of possible undescribed cryptic diversity but also because an expanded morphological revision is lacking. We suggest an integrative approach in order to resolve what can be seen morphological vs. molecular disagreements.

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Tables.

Table 1. Uncorrected genetic *p*-distances for COI and CYTB markers.

Species	COI Interspecific	COI Intraspecific	CYTB Interspecific	CYTB Intraspecific
Caluromys lanatus	8.5	1.9	11.6	1.8
Didelphis marsupialis	2.9	0.7	NA	NA
Marmosa isthmica	9.4	0.2	8.4	4.0
Molossops temminckii	4.9	2.3	NA	2.7
Molossus molossus	1.2	0.6	1.7	1.3
Molossus rufus	1.5	0.8	2.2	1.7
Molossus sp.	1.2	0.1	1.4	0.5
Desmodus rotundus	NA	4.2	NA	NA
Chiroderma villosum	7.3	1.2	4.3	1.1
Chiroderma sp.	5.4	0.0	3.4	0.6
Micronycteris megalotis	12.5	4.2	1.9	1.2
Phyllostomus hastatus	NA	NA	7.1	3.2
Gardnerycteris crenulatum	12.8	2.8	6.5	5.4
Lophostoma occidentalis	9.6	0,3	7.5	3.9
Uroderma covexum	1.8	1.0	1.4	0.7
Platyrrhinus helleri	4.8	3.2	2.7	0.2
Dermanura anderseni	2.8	1.3	5.7	1.2
Artibeus lituratus	1.5	0.9	4.7	1.0
Artibeus planirostris	1.5	0.8	2.6	1.6
Carollia castanea	NA	NA	3.2	0.2
Carollia perspicillata	NA	NA	2.6	1.6
Vampyressa thyone	10.0	0.7	10.0	1.7
Myotis sp	4.6	0.0	3.1	0.0
Notosciurus granatensis	NA	NA	8.9	1.4
Proechimys sp.	11.0	0.1	6.9	0.1
Min	**1.2**	**0.0**	**1.4**	**0.0**
Mean	**5.8**	**1.4**	**4.9**	**1.6**
Max	**12.8**	**4.2**	**11.6**	**5.4**

Figures.

Figure 1. Sampling locality.

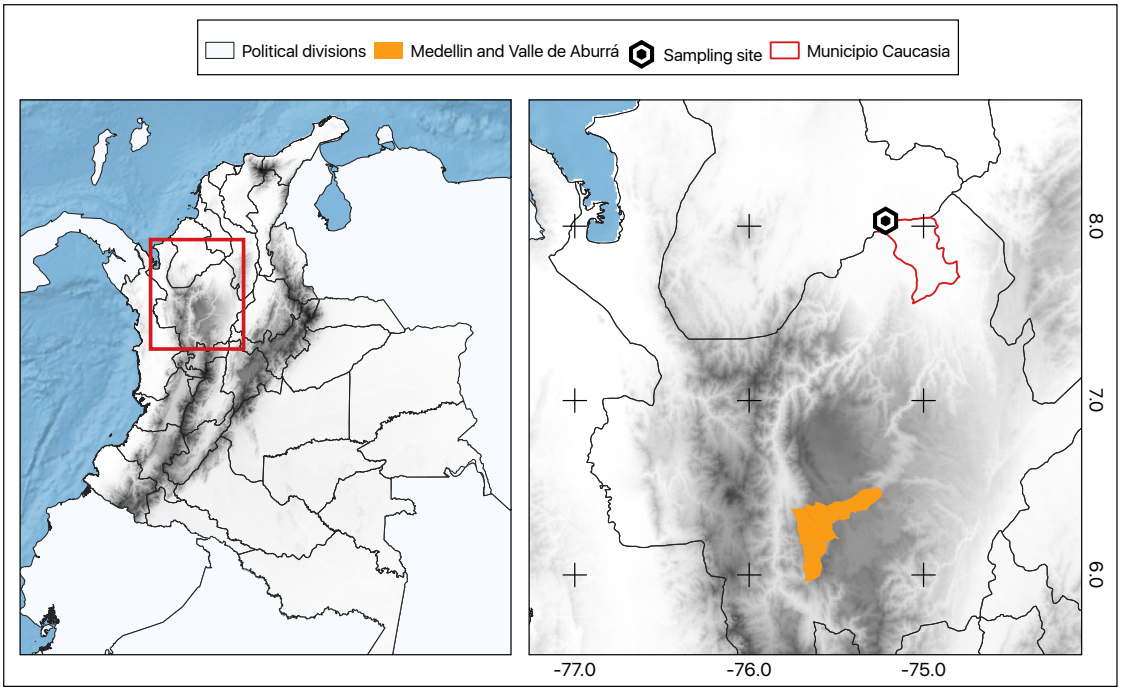

Figure 2. DNA Barcoding in the Neotropics. A) Relative abundance of each animal Class for all COI non-human records in BOLD's Public Database Portal. ("other" makes reference to classes with relative abundances less than 1%). B) Published DNA Barcoding papers in Colombia relative to Class. C) Total number of COI records in BOLD per country. D) Total number of mammalian COI sequences per country. Note that C and D do not include human sequences, numbers above bars correspond to the number of BINS, and countries with an asterisks (*) represent iBOLD member nations.

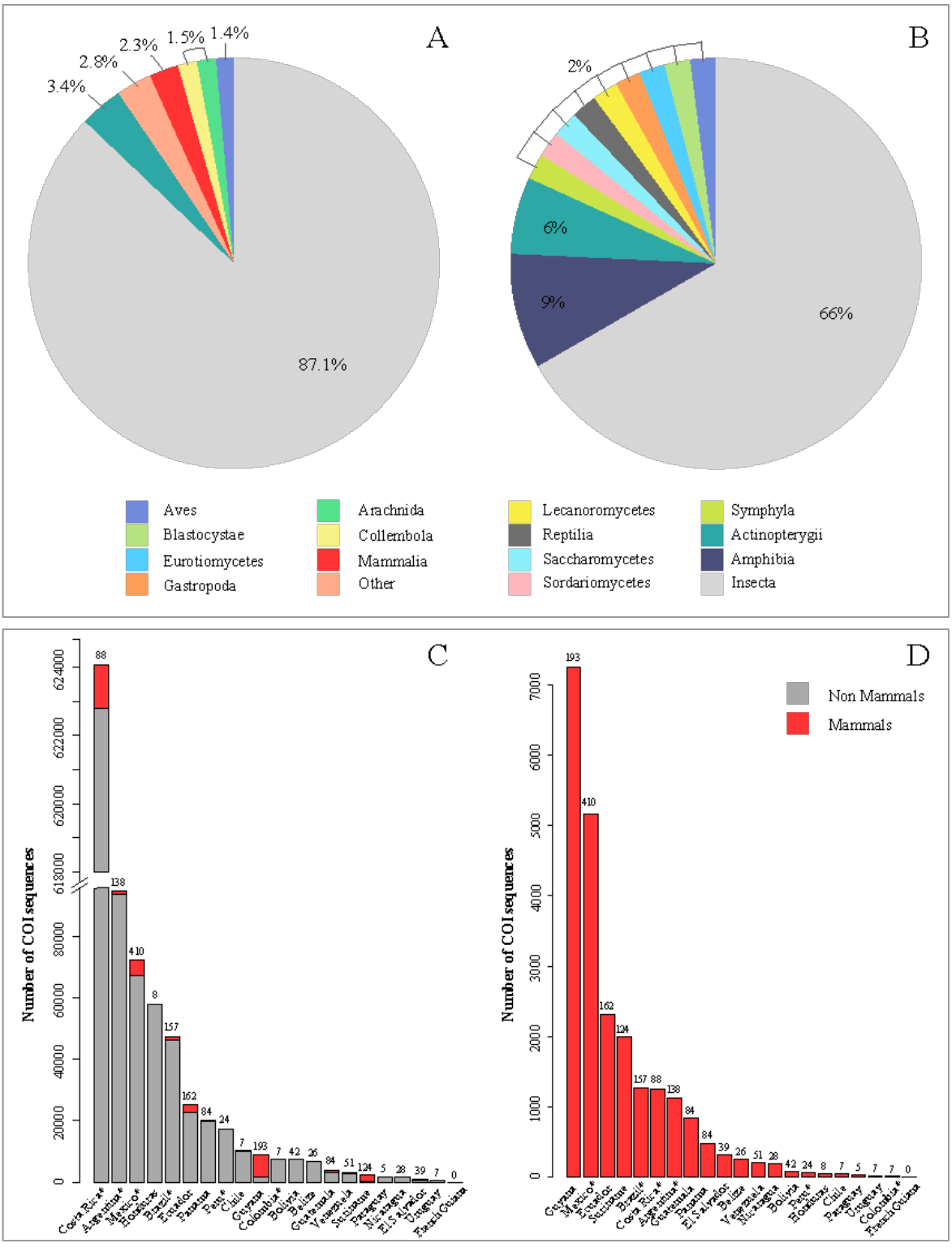

Figure 3. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Caluromys*. Bolded terminals are sequences generated in this report.

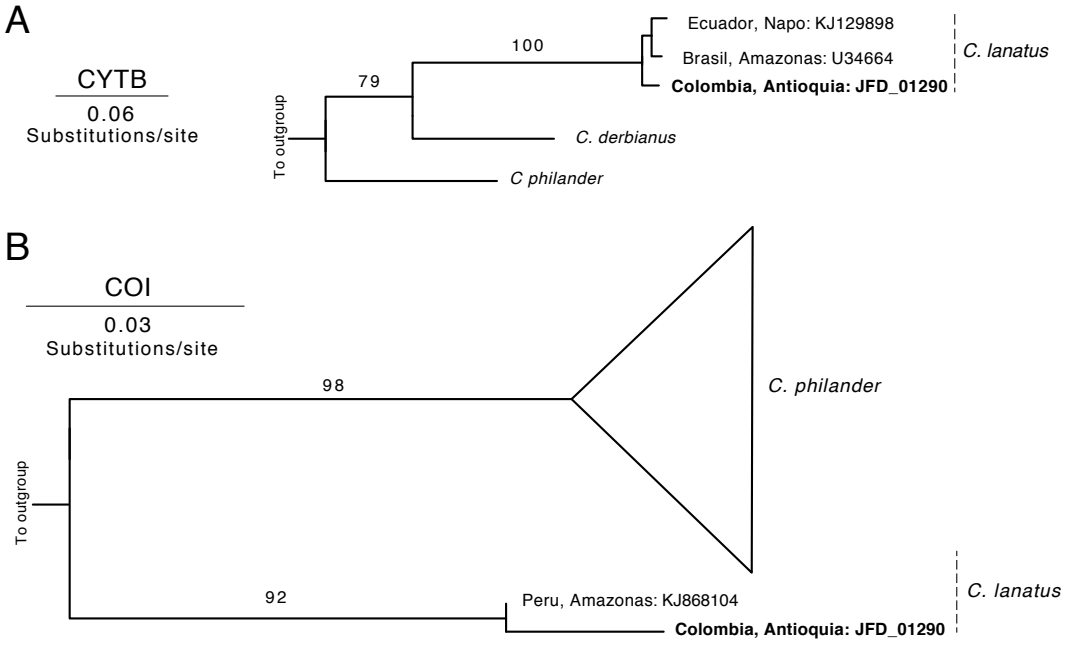

Figure 4. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Didelphis*. Bolded terminals are sequences generated in this report.

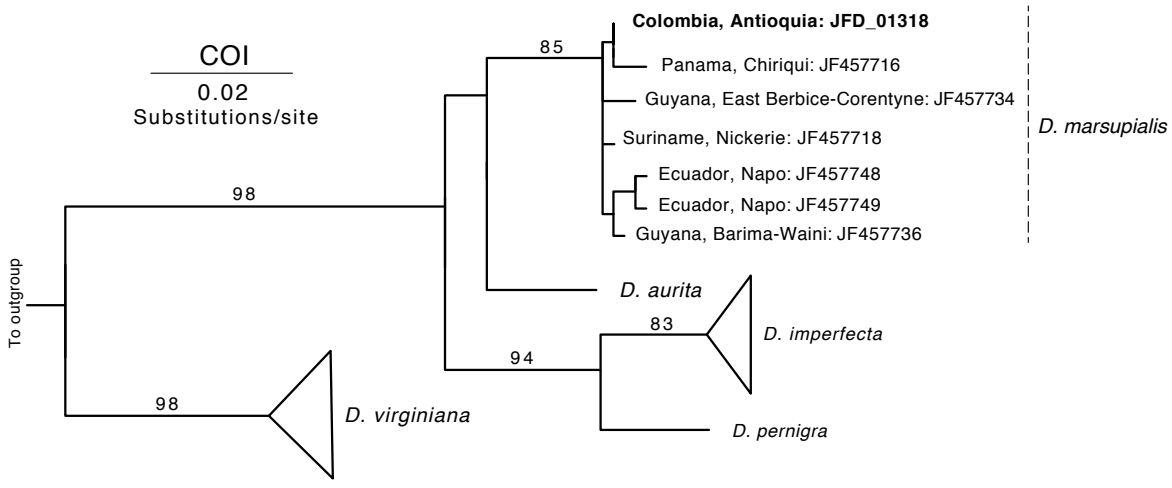

Figure 5. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Marmosa*. Bolded terminals are sequences generated in this report.

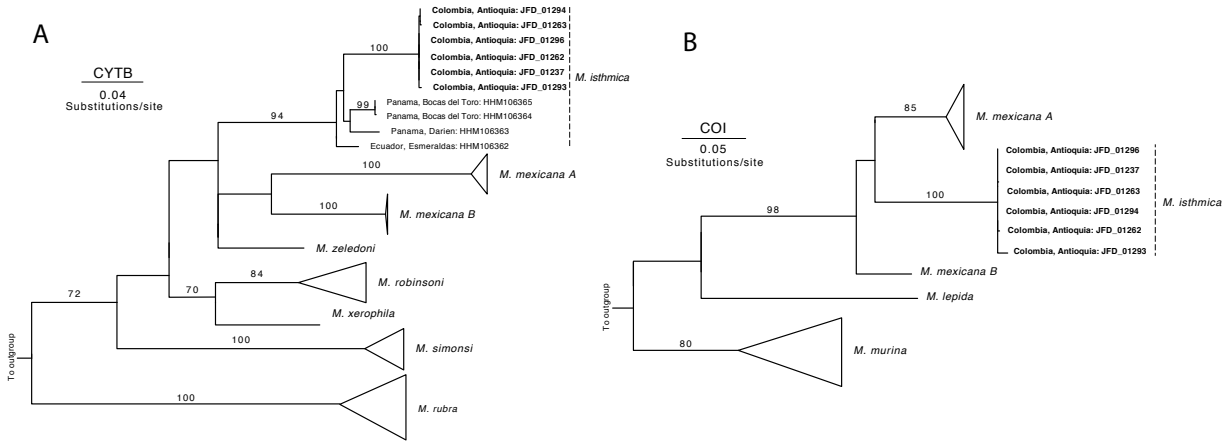

Figure 6. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Molossops*. Bolded terminals are sequences generated in this report.

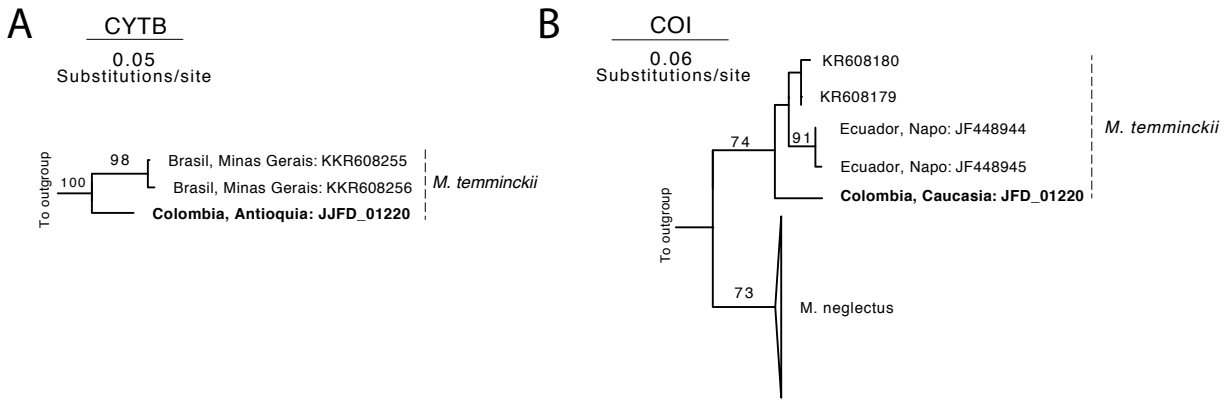

Figure 7. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Molossus*. Bolded terminals are sequences generated in this report.

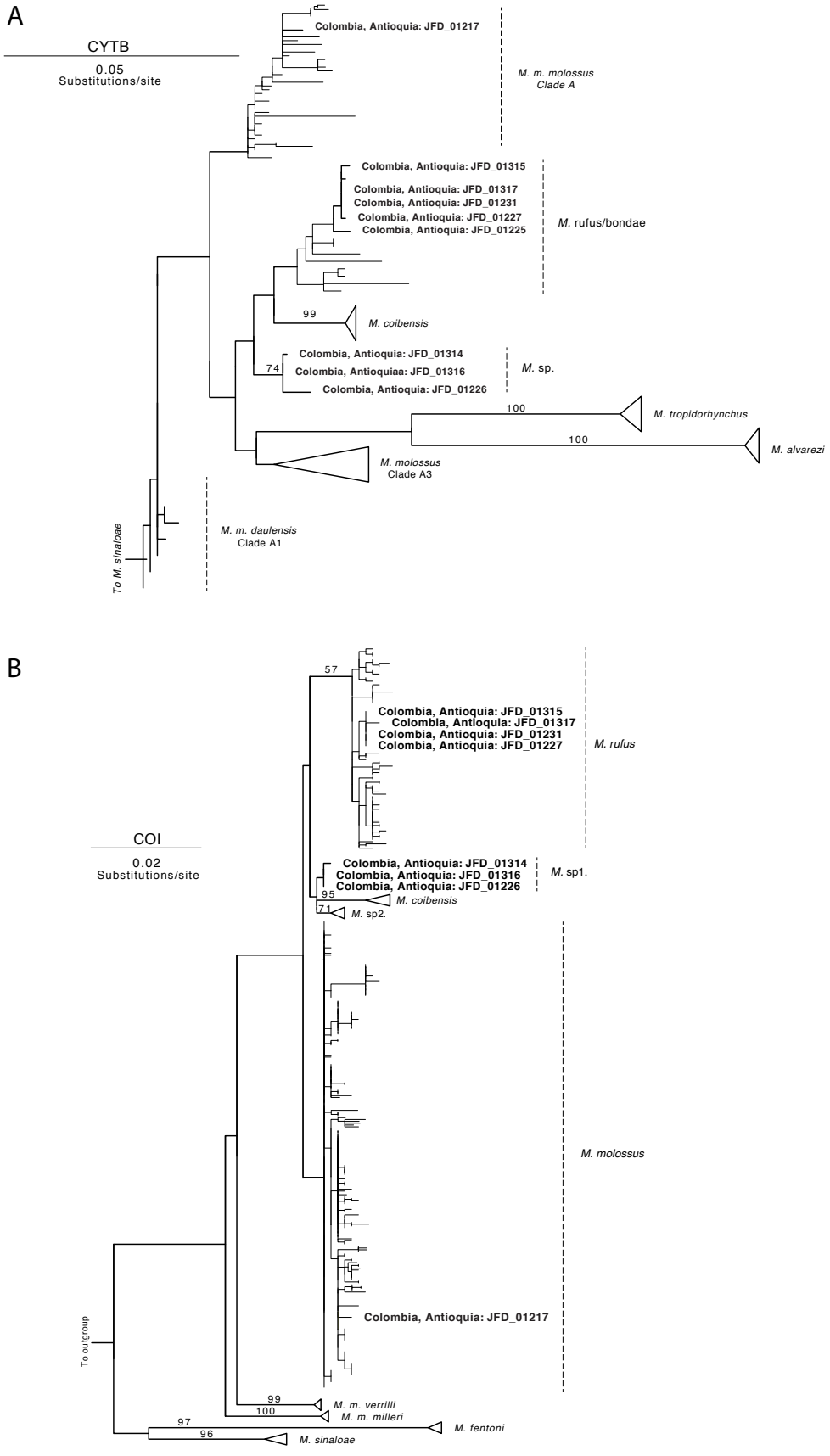

Figure 8. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Desmodus*. Bolded terminals are sequences generated in this report.

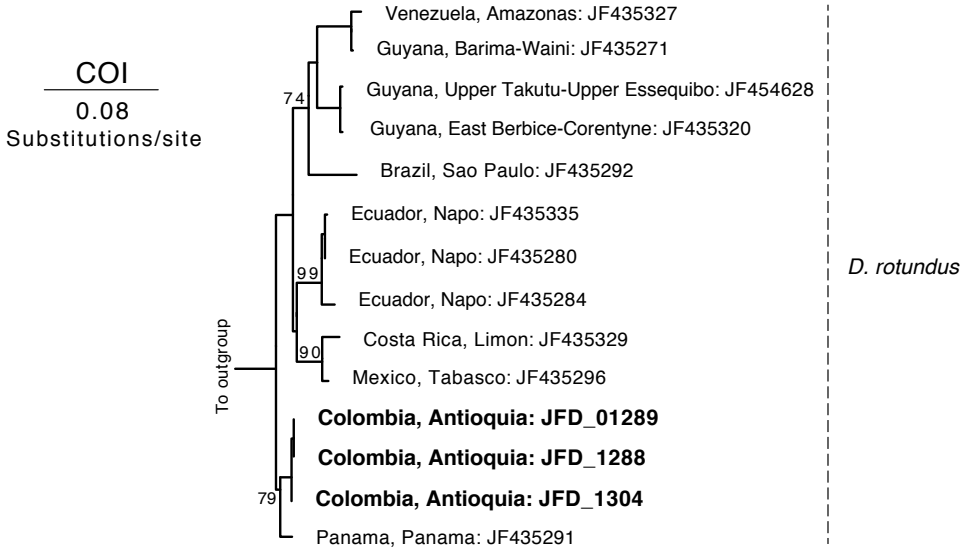

Figure 9. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Chiroderma*. Bolded terminals are sequences generated in this report.

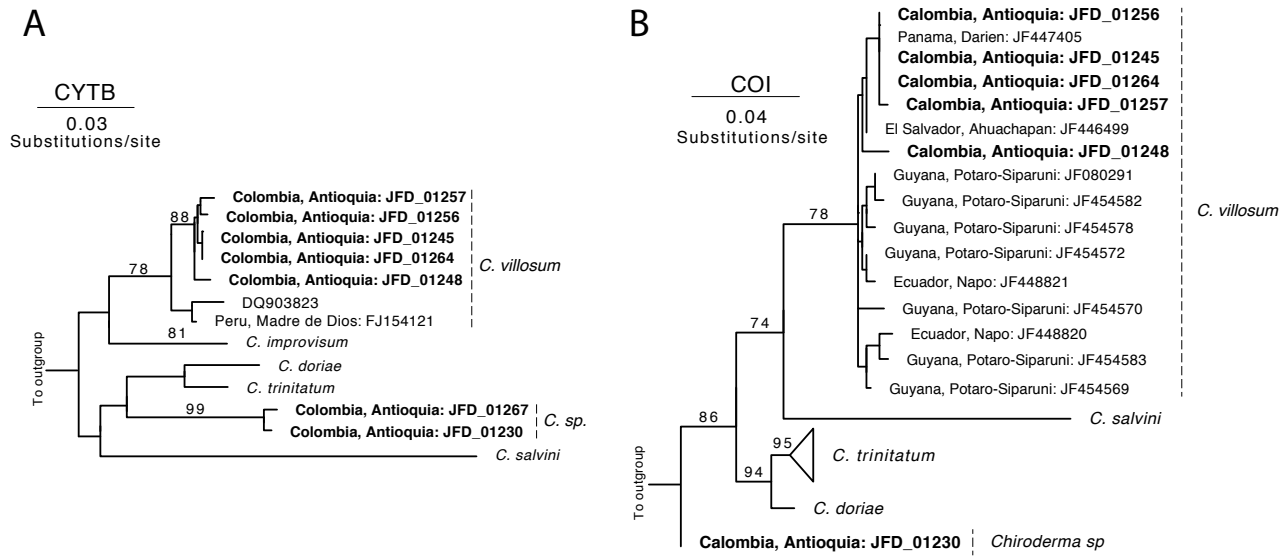

Figure 10. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Micronycteris*. Bolded terminals are sequences generated in this report.

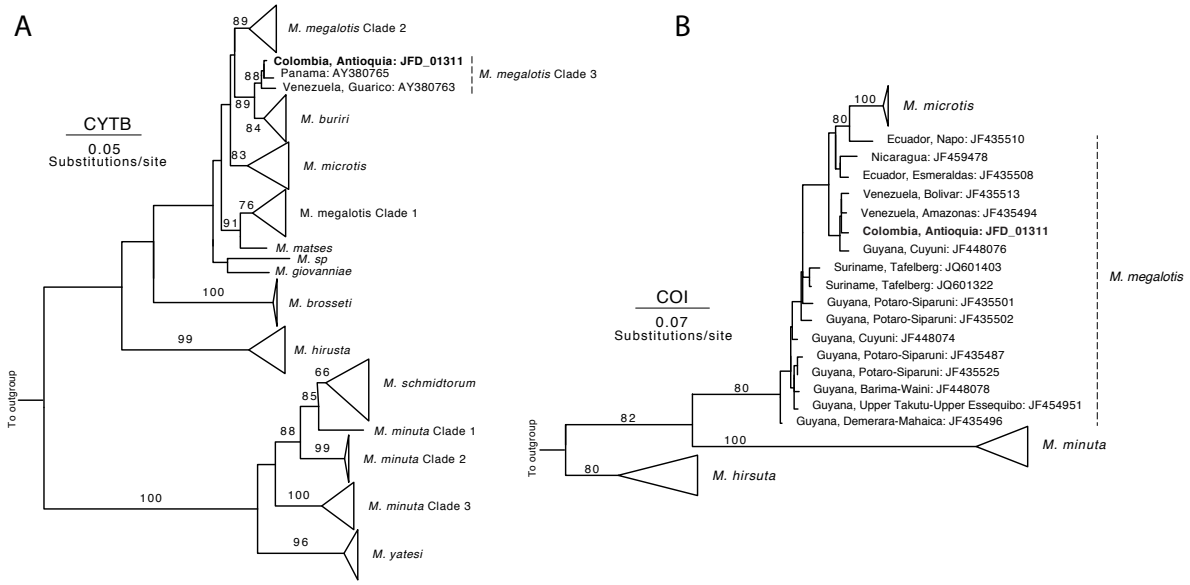

Figure 11. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Phyllostomus*. Bolded terminals are sequences generated in this report.

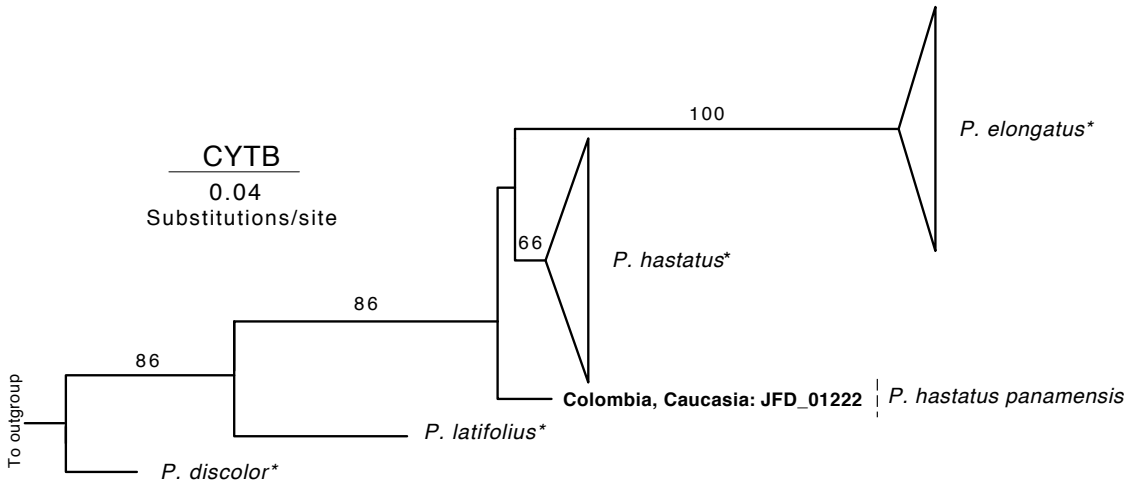

Figure 12. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Gardnerycteris*. Bolded terminals are sequences generated in this report.

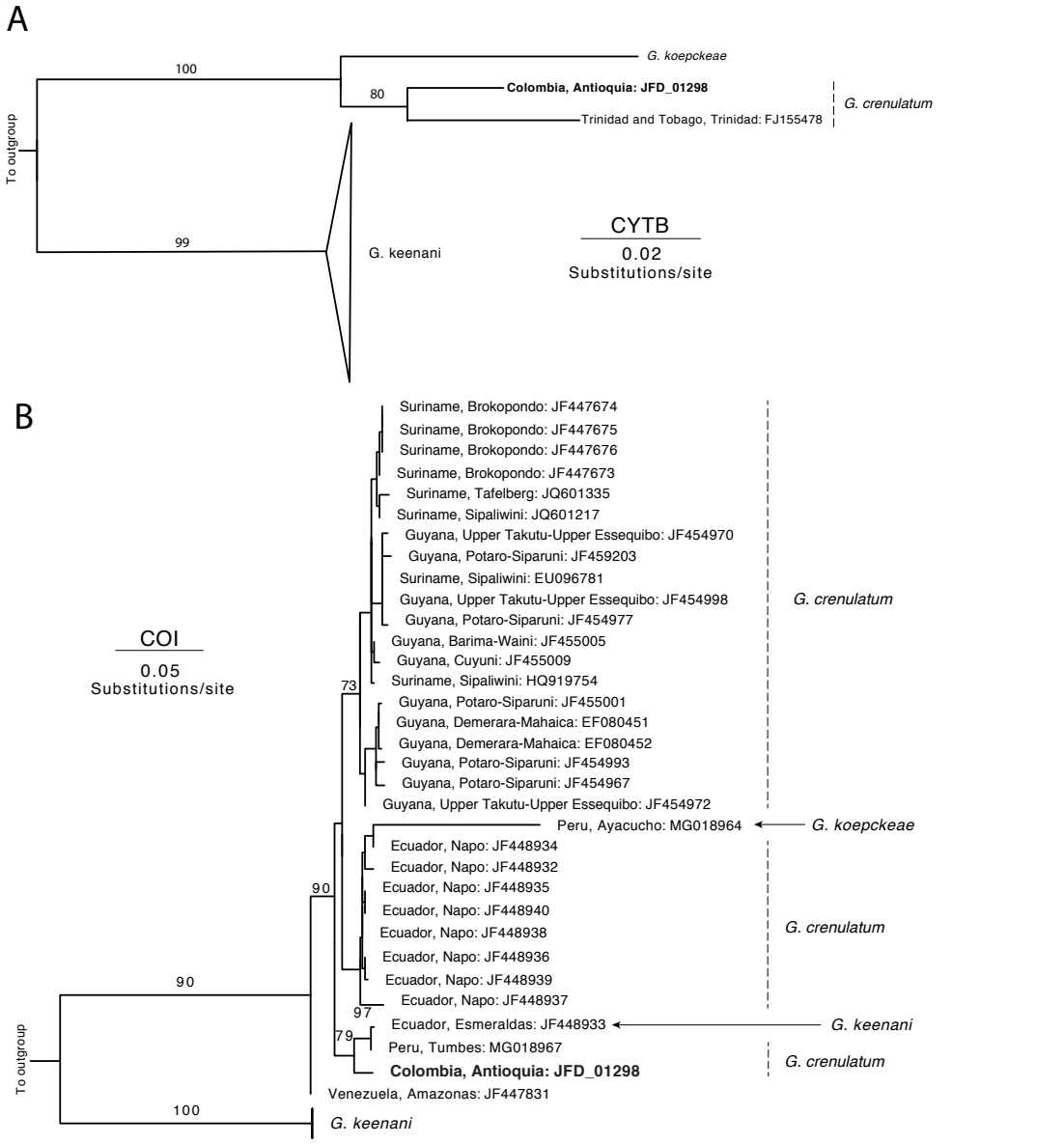

Figure 13. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Lophostoma*. Bolded terminals are sequences generated in this report.

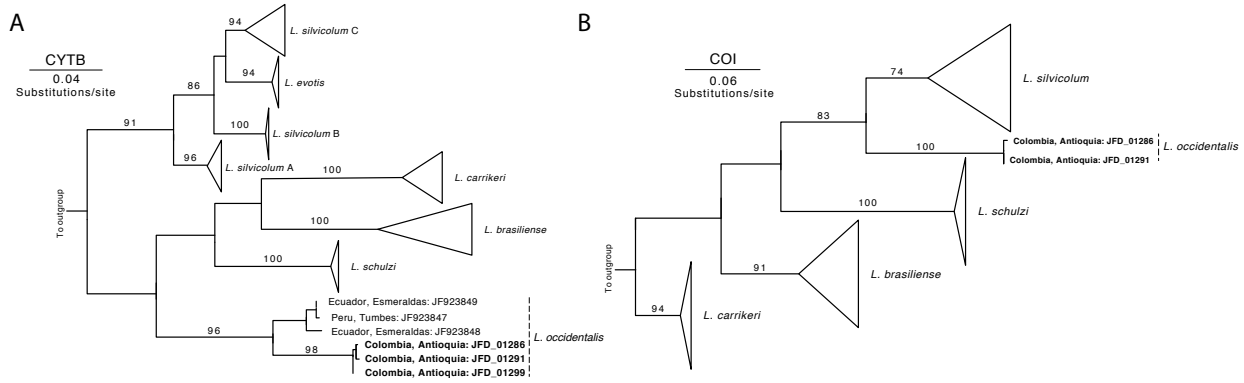

Figure 14. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Uroderma*. Bolded terminals are sequences generated in this report.

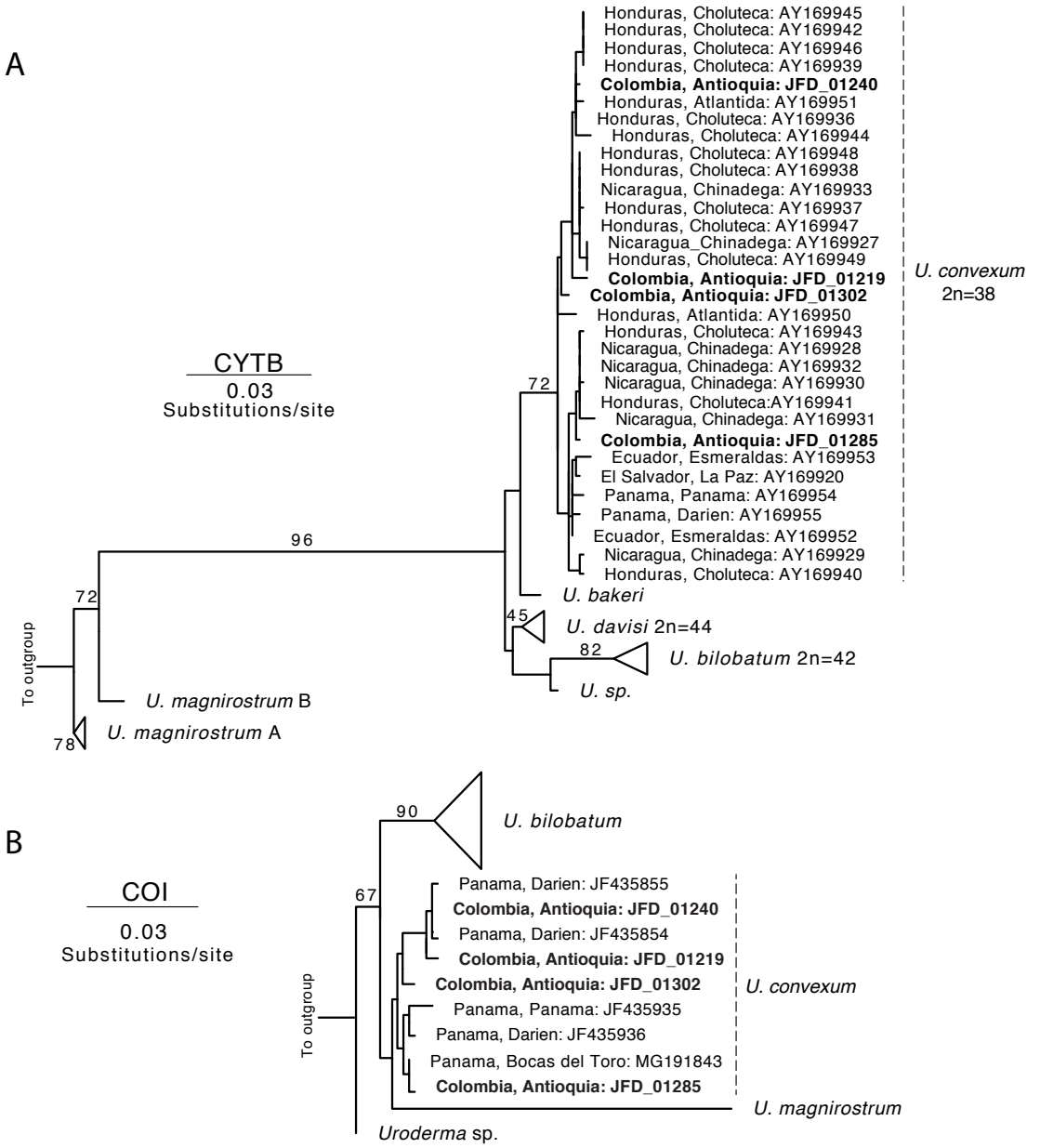

Figure 15. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Platyrrhinus*. Bolded terminals are sequences generated in this report.

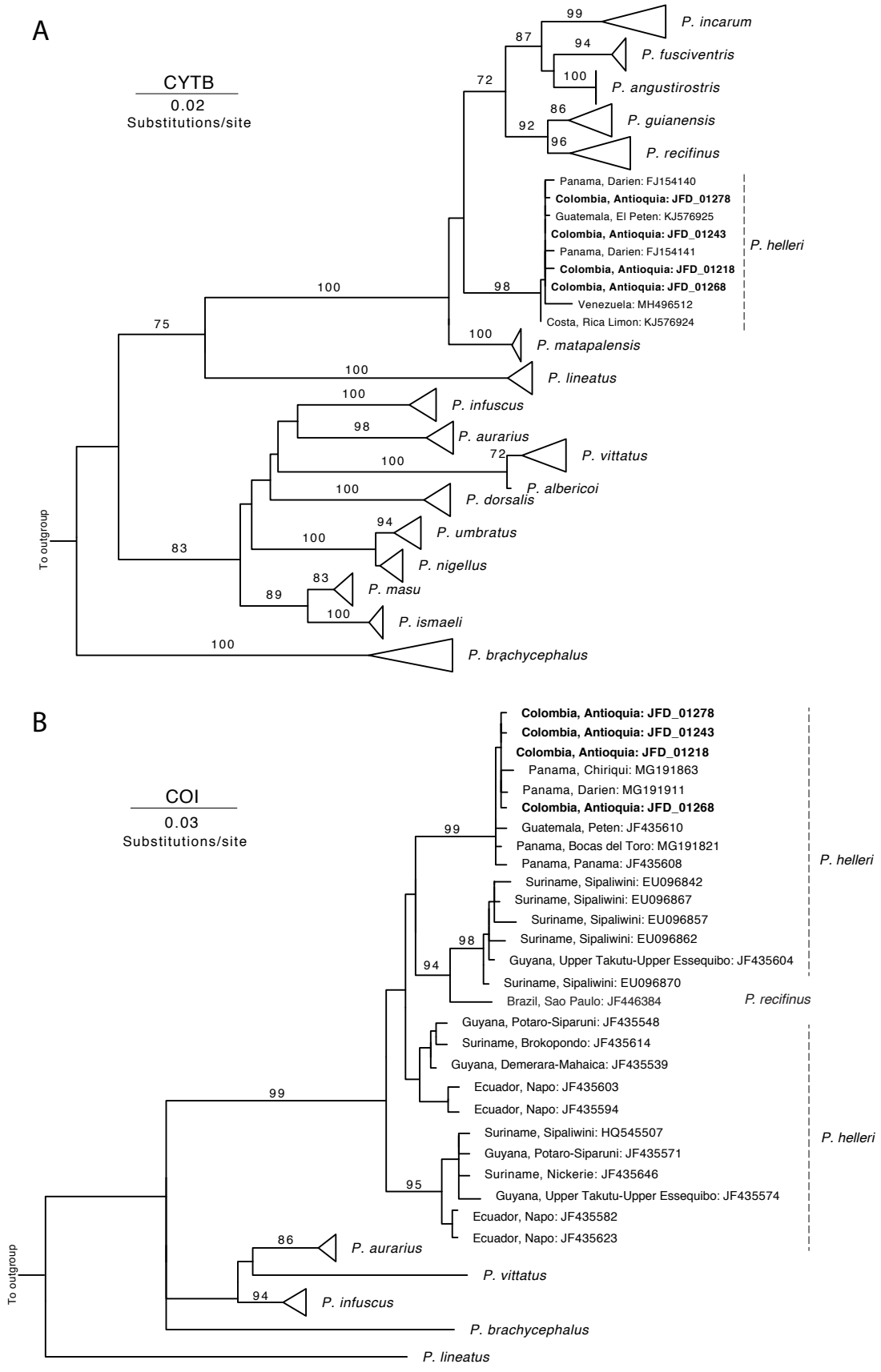

Figure 16. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Vampyressa*. Bolded terminals are sequences generated in this report.

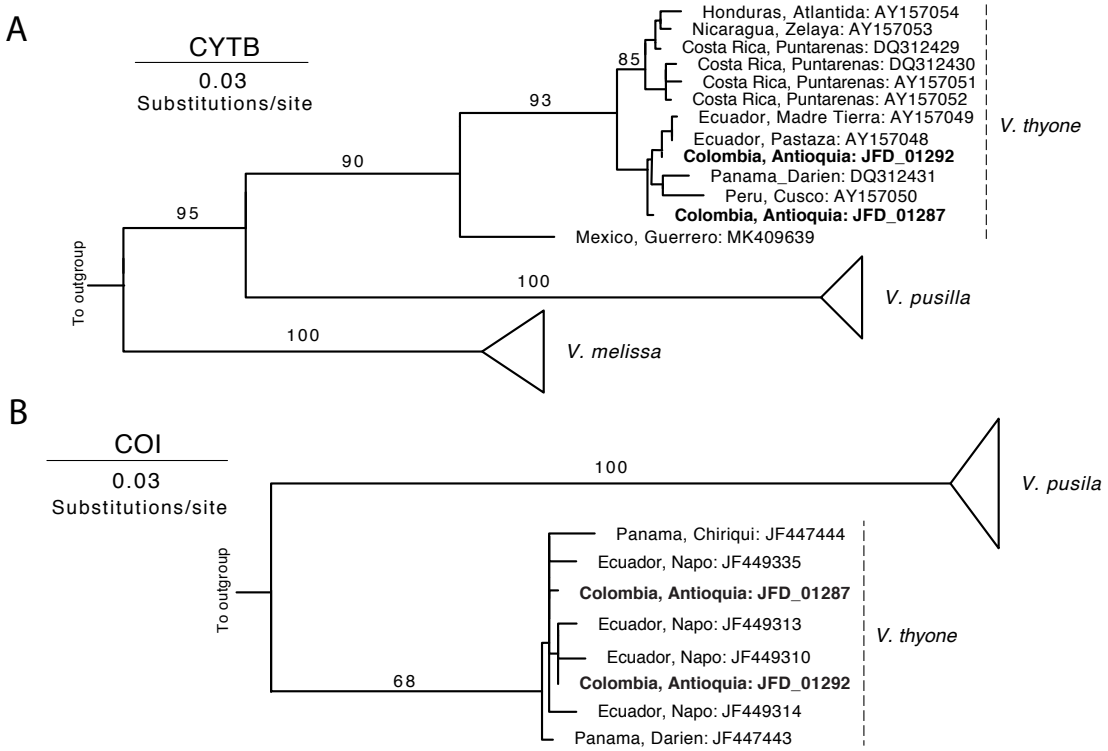

Figure 17. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Carollia*. Bolded terminals are sequences generated in this report.

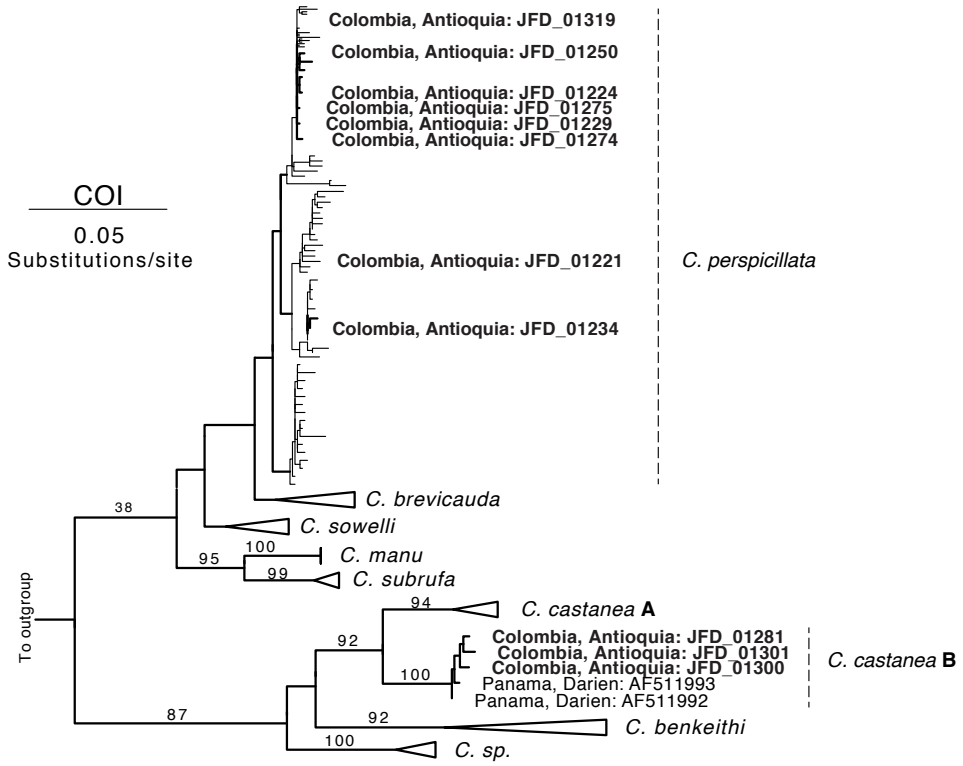

Figure 18. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Artibeus*. Bolded terminals are sequences generated in this report.

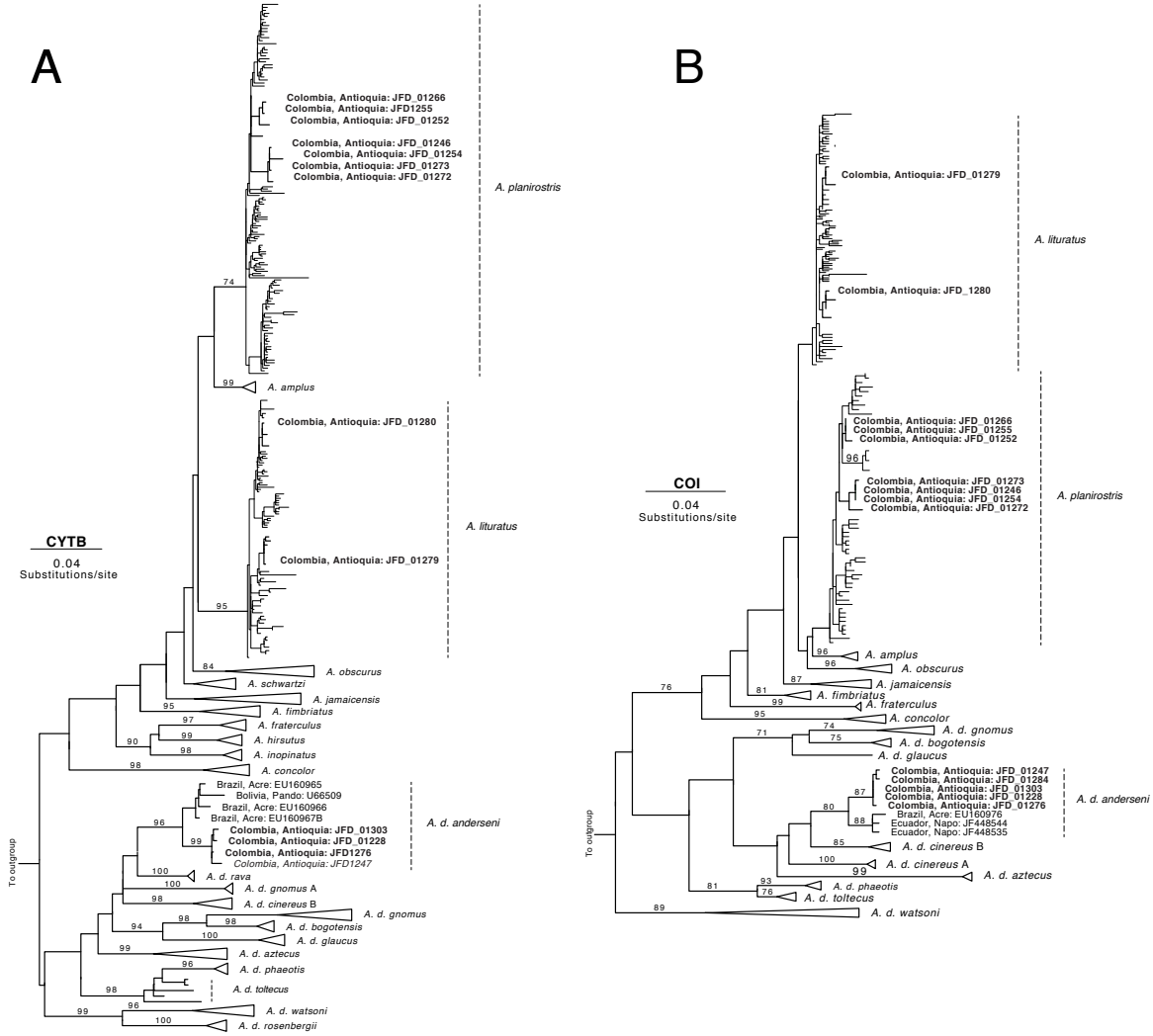

Figure 19. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Myotis*. Bolded terminals are sequences generated in this report.

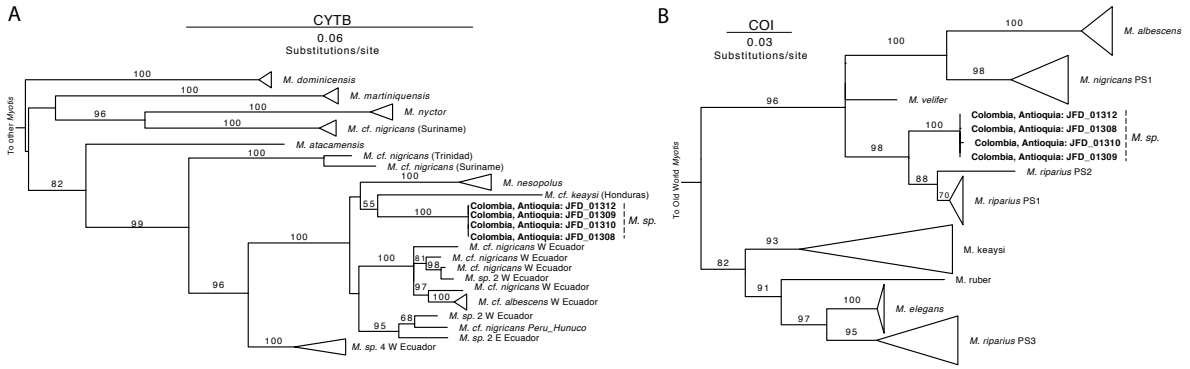

Figure 20. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Notosciurus*. Bolded terminals are sequences generated in this report.

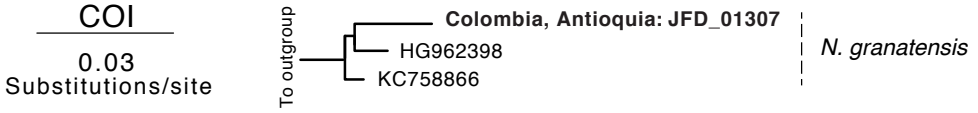

Figure 21. Maximum likelihood topology of mitochondrial DNA sequences of the genus *Proechimys*. Bolded terminals are sequences generated in this report.