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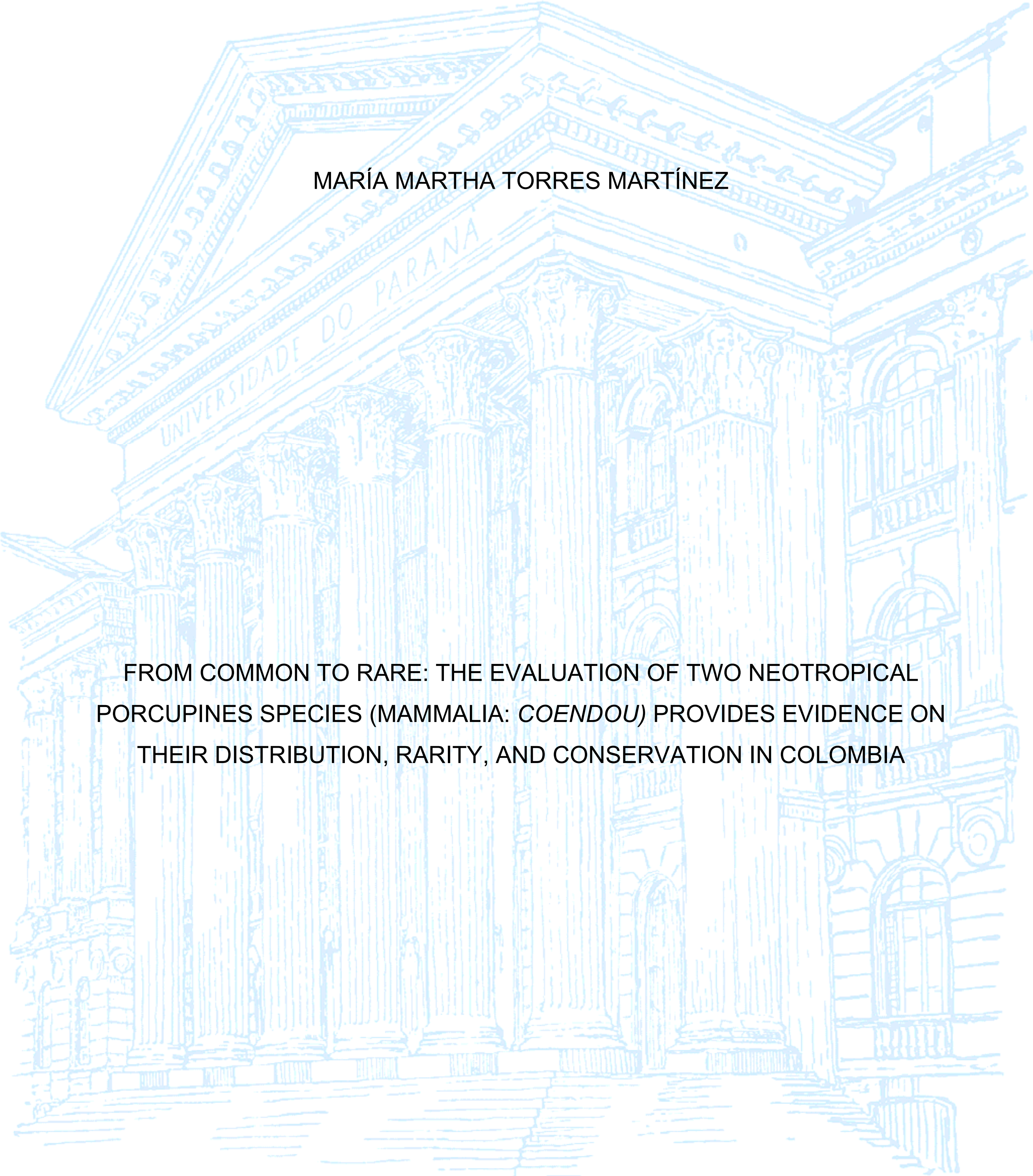

MARÍA MARTHA TORRES MARTÍNEZ

FROM COMMON TO RARE: THE EVALUATION OF TWO NEOTROPICAL PORCUPINES SPECIES (MAMMALIA: *COENDOU)* PROVIDES EVIDENCE ON THEIR DISTRIBUTION, RARITY, AND CONSERVATION IN COLOMBIA

CURITIBA
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Dissertação apresentada como requisito parcial à obtenção do grau de Mestre em Ecologia & Conservação, no Curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, da Universidade Federal do Paraná.

Orientador: Prof. Dr. Fernando C. Passos
Co-orientador: Prof. Dr. Héctor E. Ramírez-Chaves

CURITIBA
2018

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(Telma Terezinha Stresser de Assis –CRB/9-944)

Martínez, María Martha Torres
From commom to rare: the evaluation of two neotropical porcupines species (Mammalia: *Coendou*) provides evidence on their distribution, rarity, and conservation in Colombia. – Curitiba, 2018.
80 p.: il. ; 30cm.

Orientador: Fernando C. Passos
Co-orientador: Héctor E. Ramírez-Chaves
Dissertação (Mestrado) - Universidade Federal do Paraná, Setor de Ciências Biológicas. Programa de Pós-Graduação em Ecologia e Conservação.

1. Mamífero. 2. Ecologia. 3. Genética. 4. Taxonomia. I. Título. II. Passos, Fernando C. III. Ramírez-Chaves, Héctor E. IV. Universidade Federal do Paraná. Setor de Ciências Biológicas. Programa de Pós-Graduação em Ecologia e Conservação.

CDD (20. ed.) 591.5

MINISTÉRIO DA EDUCAÇÃO
SETOR CIÊNCIAS BIOLÓGICAS
UNIVERSIDADE FEDERAL DO PARANÁ
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO ECOLOGIA E CONSERVAÇÃO

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Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da dissertação de Mestrado de **MARIA MARTHA TORRES MARTINEZ** intitulada: **FROM COMMON TO RARE: THE EVALUATION OF TWO NEOTROPICAL PORCUPINES SPECIES (MAMMALIA: COENDOU) PROVIDES EVIDENCE ON THEIR DISTRIBUTION, RARITY, AND CONSERVATION IN COLOMBIA**, após terem inquirido a aluna e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 26 de Fevereiro de 2018.

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Avaliador Externo (UFPR)

AGRADECIMENTOS

Ao meu orientador, Prof. Dr. Fernando C. Passos, pela oportunidade de fazer parte do seu laboratório, acompahamento e orientação.

Ao meu co-orientador, Prof. Dr. Héctor E. Ramírez-Chaves, pelo acompahamento, orientação e paciência.

Ao Curso de Pós-Graduação em Ecologia & Conservação, do Setor de Ciências Biológicas, da Universidade Federal do Paraná, na pessoa do seu coordenador Prof. Dr. André Padial, pelo apoio recebido.

Ao Colegiado do Curso de Pós-Graduação em Ecologia & Conservação, pela compreensão e apoio aos momentos difíceis.

Aos colegas do laboratório (LABCEAS) pela colaboração e apoio neste processo, especialmente ao Luiz H. Varzinczak.

A Dr. Elkin Noguera A. Noguera-Urbano, Javier E. Colmenares-Pinzón e Javier García pelas contribuições e sugestões no trabalho.

RESUMO

Os porcos-espinhos do gênero *Coendou* são alguns dos mamíferos menos estudados do Neotrópico, distribuídos desde o sul do México até o norte da Argentina, com espécies de distribuição tanto ampla quanto restrita. No caso da espécie *Coendou vestitus*, sua ocorrência está restrita aos Andes da Colômbia com pouca informação sobre sua distribuição, ecologia e conservação. Portanto, não há programas de conservação e sua atual categoria de ameaça é controversa. Em contraste, a espécie *Coendou prehensilis* é amplamente distribuída na América do Sul. No entanto, ainda há dúvidas sobre sua distribuição e taxonomia, especialmente na Colômbia. Por exemplo, sua presença na região amazônica foi sugerida com base em registros de países vizinhos, como o Equador, Venezuela e Brasil, mas até o momento não há registros confirmados que validem sua presença nessa região da Colômbia. Com base nisso, avaliamos o estado de conhecimento, distribuição e raridade, e novas informações genéticas de *C. vestitus*, com o objetivo de consolidar a informação para uma nova avaliação da sua categoria de ameaça (Capítulo I). Além disso, a distribuição de *C. prehensilis* na Colômbia é atualizada e novas informações genéticas contribuíram para esclarecer alguns problemas taxonômicos fornecidos (Capítulo II). Para isso (Capítulo I), literatura e espécimes em museus na Colômbia foram revisados. Com esta informação, a extensão da ocorrência (EOO) e área de ocupação (AOO) para *C. vestitus* foi calculada com dados das localidades em que obtivemos registros da espécie. Um modelo Maxent foi construído com o objetivo de estimar áreas com condições ambientais semelhantes. Além disso, uma sequência do citocromo b de *C. vestitus* foi obtida do registro mais recente. Para *C. prehensilis* (Capítulo II), foram analisados espécimes depositados em coleções colombianas, registros fotográficos e literatura para confirmar a presença de *C. prehensilis* na Amazônia colombiana e atualizar sua distribuição, além da utilização de uma nova sequência do citocromo b para esclarecimento taxonômico.

Para *C. vestitus* (Capítulo I) foram encontradas 14 publicações que possuem informações relacionadas principalmente à taxonomia e distribuição. Sua ocorrência foi confirmada em três localidades da Cordilheira Oriental colombiana. A espécie apresenta um EOO de 1.195 km^2 e AOO de 12 km^2. *C. vestitus* mostra o maior grau de raridade devido à sua pequena área de distribuição, baixa densidade populacional estimada, número reduzido de habitats ocupados e pequeno tamanho corporal. Com base nessas informações, sugerimos transferir a categoria de ameaça global de Dados insuficientes (Data Defficient, DD) para Em Perigo (Endangered, EN). Para *C. prehensilis* (Capítulo II), novos registros foram encontrados mostrando que esta é a espécie que habita maior quantidade de regiões naturais e sete províncias biogeográficas na Colômbia, enquanto outras espécies estão restritas a uma ou duas províncias. A sequência do citocromo b é aninhada com sequências adicionais de outras localidades, fornecendo mais informações que esclarece sua taxonomia.

Em conclusão, esta dissertação fornece informações que contribuem para o conhecimento do gênero *Coendou* na América e, principalmente, na Colômbia. Estes novos dados podem ser usados para esclarecer aspectos como a distribuição, morfologia, sistemática, genética e conservação de espécies do gênero.

Palavras-chave: Amazônia, Andes, Coleções biológicas, Ecologia, Genética, Modelos de distribuição, Porco-espinho, Taxonomia.

ABSTRACT

The porcupines of the genus *Coendou* are some of the least studied mammals of the Neotropics distributed from the south of Mexico to the north of Argentina, including both species of wide or restricted distribution. In the case of the brown hairy dwarf porcupine *Coendou vestitus*, its distribution is restricted to the Andes of Colombia with little information on its actual presence, ecology, or conservation. Therefore, there are no conservation programs and its current threaten category is controversial. In contrast, the Brazilian porcupine *Coendou prehensilis* is widely distributed South America, however there are still some doubts about its distribution and taxonomy, especially in Colombia. For example, its presence in the Amazon region has been suggested based on records from bordering countries such as Ecuador, Venezuela and Brazil, but until now, there are no confirmed records that validate its presence in that region of Colombia. Based on that, here the state of knowledge, distribution and rarity is evaluated, and new genetic information of *C. vestitus*, is provided aiming to consolidate information for a reassessment of its threaten category (Chapter I). Furthermore, the distribution of *C. prehensilis* in Colombia is updated and new genetic information to contribute to clarify some taxonomic problems iss provided (Chapter II). For this (Chapter I), a literature and specimens in museums in Colombia were reviewed. With this information, the extent of occurrence (EOO) and occupation area (AOO) for *C. vestitus* was calculated with data from the corroborated localities. A Maxent model was constructed with the purpose of estimating areas with similar environmental conditions. In addition, a cytochrome b sequence of *C. vestitus* was obtained form the the most recent record. For *C. prehensilis* (Chapter II) specimens deposited in Colombian collections, photographic records and literature to confirm the presence of *C. prehensilis* in the Colombian Amazon and update the distribution, besides the use of a new cytochrome b sequence for taxonomic clarification. .

For *C. vestitus* (Chapter I) 14 publications that have information related mainly to the taxonomy and distributionwere found. Its occurrence was confirmed in three localities of the Eastern Cordillera. The species presents an EOO of 1,195 km2 and AOO of 12 km2*.* *C. vestitus* shows the highest degree of rarity due to its small area of distribution, low estimated population density, number of occupied habitats and small body size. Based on this information, we suggest transferring the global threat category from Insufficient Data (DD) to Endangered (EN). For *C. prehensilis* (Chapter II), new records were found showing that this is the species that inhabits more natural regions and seven biogeographic provinces in Colombia, while other species are restricted to one or two provinces. The cythocrome b sequence is nested with additional sequences from other localities, providing more information that clarifies its taxonomy.

In conclusion, this dissertation provides information that contributes to the knowledge of the genus *Coendou* in America, mainly in Colombia, and that can be used to clarify aspects such as the distribution, morphology, systematics, genetics and conservation of species of the genus.

Key-words: Amazon, Andes, Biological collections, Ecology, Genetics,
Distribution models, Porcupine, Taxonomy.

SUMÁRIO

I INTRODUCTION

Species distributions are influenced by historical, evolutionary and ecological processes acting at different intensities and spatial scales (Soberón & Peterson 2005; Soberón & Nakamura 2009). Among these factors are the biotic and abiotic conditions, including the distribution and evolution of populations to adapt to the new conditions (Anderson et al. 2002, Peterson & Soberón 2012, Soberón 2010, Soberón & Nakamura 2009, Soberón & Peterson 2005, Violle et al. 2014). In the last decades, new tools such as Species Distribution Models (SDM) have become helpful in clarifying how abiotic factors shape the distribution of certain species. In turn, this tool allows the estimation of the current or potential distribution of the species, or the set of their suitable habitats (Soberón 2010, Soberón & Nakamura 2009, Soberón & Peterson 2005). In a context of Neotropical Mammalogy, SDMs (Ortega-Andrade et al. 2015, Rodríquez-Soto et al. 2011) have contributed to generate new information on the distribution, ecology, and conservation of little-known species (Morato et al. 2014, Syfert et al. 2014).

In the New World, porcupines of the genus *Coendou* (Mammalia: Erethizontidae) are represented by approximately 15 species (Voss 2015, Ramírez-Chaves et al. 2016) distributed from the southern regions of Mexico, to Uruguay and northern Argentina, encompassing an elevational range between 0 and 3400 m (Ramírez-Chaves et al. 2016, Voss 2011, Voss 2015, Voss & Angermann 1997). *Coendou* represents an adaptative radiation of Neotropical arboreal mammals, being associated to several types of ecosystems, including tropical forests and subtropics, from mature to disturbed areas (Voss 2015, Voss & Angermann 1997). Although in recent years there has been an increase in the information concerning the taxonomy and natural history of this genus for specific regions (e.g. Caldara Junior & Leite

2012, Ramírez-Chaves et al. 2016, Voss 2011, 2015, Voss & Angermann 1997, Voss et al. 2013), there are still gaps in knowledge about their distribution, ecology, natural history, and conservation status. For that reason, Neotropical porcupines have been listed among the New World mammals with greatest lack of information (Voss 2011), and their conservation status is still in need of research due the scarity of basic biological information (Ramírez-Chaves et al. 2016, Voss 2011).

Recent reviews (e.g. Voss 2015) have improved the knowledge on the geographical distribution of *Coendou* species in America, as well as on their evolutionary and biogeographical relationships (Voss et al. 2013). For example, large-sized species of *Coendou* have wider distributions (e.g. Brazilian porcupine *Coendou prehensilis*), encompassing a large proportion of the South America (see Voss 2015). In contrast, small-sized species (e.g. brown hairy dwarf porcupine *Coendou vestitus*) appear to have highly restricted geographical distributions, even though there are no natural barriers that limit their distributions. In particular, *C. vestitus* is perhaps the rarest species of the genus, endemic of Colombia, and considered Vulnerable (VU) in Colombia (Alberico & Moreno 2006), but Data Deficient (DD) according to the Internacional Union for Conservation of Nature (Weksler et al. 2016). The opposite case is exemplified by *C. prehensilis*, perhaps the most common species of this genus and listed as Least Concern (LC) globally (Marinho-Filho & Emmons 2016, Ramírez-Chaves et al. 2016). Both species have different and contrasting cranial and external characters (e.g. body size, type of fur, level of inflation of the frontal sinuses) that might be influencing their distributions. However, no study to date explored the factors underlying the current distribution of *Coendou* species, mostly due to the scarcity of records for rare species. Therefore, species distribution models can provide information to fullfill the lack of records and can be used to assess threat categories.

For those reasons, the objective of this dissertation was to provide new information on the distribution, morphology, genetics, rarity and conservation status of *C. prehensilis* and *C. vestitus* in Colombia. This dissertation is presented in two chapters organized as independent manuscripts. The first chapter addressed the state of knowledge, distribution, phyogenetic position, rarity and conservation of *C. vestitus*. This manuscript was submitted to Oryx - The International Journal of Conservation. The second chapter addressed the distribution and taxonomy of *C. prehensilis* in Colombia, providing local information that shows that even for common species there are large information gaps, and it is expected to be submitted to Mastozoología Neotropical. This information is intended to contribute to fill gaps of information distribution, ecology and conservation on both species. It also aims to generate a baseline for subsequent studies involving all the species of *Coendou*.

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III

CHAPTER I

State of knowledge, distribution, rarity and conservation of the Colombian endemic Brown Hairy Dwarf Porcupine *Coendou vestitus* (Mammalia: Rodentia)

Manuscript submitted to the journal Oryx - The International Journal of Conservation

State of knowledge, distribution, rarity and conservation of the Colombian endemic Brown Hairy Dwarf Porcupine *Coendou vestitus* (Mammalia: Rodentia)

Abstract

The Brown Dwarf porcupine *Coendou vestitus* is a poorly studied endemic Andean species of Colombia. This has limited the implementation of conservation programs. Its current threat category is contradictory; globally it has been classified as Data Deficient (DD), however, in Colombia is currently categorized as Vulnerable. We update the state of knowledge, distribution and rarity, and provide consolidated information for a new assessment of its threat category. For this, we reviewed literature and vouchers housed in natural history collections of Colombia. We used confirmed records to estimate the Extent of Ocurrence (EOO) and the Area of Occupancy (AOO) based on the minimum convex polygon (MCP) for this species. Additionally, we used the principle of maximum entropy (Maxent) to estimate similar environmental conditions, and we provided molecular data for the most recent record. We found 14 published works related to *C. vestitus*. The most recurrent research topics (11 publications) were “Taxonomy and Systematics”, and “Biogeography, distribution and records”. Its occurrence was confirmed in three localities in the Eastern Cordillera. The species has an EOO of 1,195 km^2, and AOO of 12 km^2. *Coendou vestitus* exhibits the highest degree of rarity due to its small distribution area, estimated low population density, habitats occupied, and small body size. Based on this information, we suggest the transference of the global threat category from DD to Endangered (EN). This new category will help to focus research and conservation efforts, considering that *C. vestitus* is the porcupine with the most restricted distribution in America that inhabits one of the most endangered ecosystems globally.

Key words: Andes, distribution models, ecology, taxonomy, vouchers.

Introduction

The Brown Hairy Dwarf Porcupine *Coendou vestitus* Thomas, 1899 is perhaps one of the rarest of the seven species of porcupines (genus *Coendou*) that occur in Colombia (Ramírez-Chaves et al., 2016). It is a small species (head and body length: 330-370 mm), characterized by having three different types of fur: long dorsal fur, bicolored defensive fur, and bristle-quills (Voss, 2015). It is endemic to both sides of the Eastern Cordillera, and since its description more than a century ago (Thomas, 1899), it has been recorded only from less than five localities. There are mentions of its presence in the departments of Boyacá (Villa de Leyva), Cundinamarca (Quipile and San Juan de Rio Seco), and Meta (Villavicencio; Alberico et al., 1999; Voss & da Silva, 2001; Ramírez-Chaves et al., 2016; Weksler et al., 2016). However, only two of these localities, both in the western foothills of the Eastern Cordillera in the Department of Cundinamarca, are definitely identifiable (Voss, 2015), whereas in at least two other localities (Villavicencio and Villa de Leyva) its occurrence is controversial or lacks detailed information. Its rarity has not been evaluated as well, and it has been suggested based only in the absence of voucher specimens and its presence only in few localities. Information on its ecology, genetics, natural history and conservation status is also scarce, and in the case of the latter, controversial. For example, globally it has been categorized as Data Deficient (DD) by The IUCN Red List of Threatened Species (Weksler et al., 2016), because the species is only known from two localities. However, in the same account, three localities in total are mentioned. At the national level, the species has been listed as Vulnerable (VU) based on the reduced distribution area, and habitat loss and fragmentation (Alberico & Moreno, 2006), and it is the only porcupine species listed in a threat category in Colombia.

Considering the scarcity of records, additional tools can be used to estimate the distribution of *C. vestitus*. An alternative is to use Species Distribution Models (SDM) that have been developed to overcome the lack of distributional data and to deal with few samples to approximate the environmental conditions that a species can inhabit (Guisan & Zimmermann, 2000; Pearson et al., 2007; Shcheglovitova & Anderson, 2013). Species distribution models relate recorded species presences to abiotic factors to estimate areas with suitable environmental conditions for populations of a species (Pearson et al., 2007; Shcheglovitova & Anderson, 2013). Although the performance of SDM is affected when using reduced samples sizes (Pearson et al., 2007), these can still provide valuable biogeographical information to identify regions that have similar environmental conditions to where the species currently maintains populations (Pearson et al., 2007; Proosdij et al., 2016).

All the problems described above have made the assessment of the distribution of *C. vestitus*, its threatened category more difficult, thus making any evaluation of the current knowledge of this endemic species an urgent priority. Therefore, to clarify these issues, we reviewed all available literature, and specimens housed in Colombia natural history museums and collections. We also use confirmed presence records for *C. vestitus* to identify regions that have similar environmental conditions to where the species is known to occur and added a new record confirmed by molecular analyses.

Methods

State of knowledge

We compiled all available information from published literature (papers, book chapters, etc) since the species description in 1899. We searched for information on the following categories used to establish the state of knowledge of endemic mammals of Colombia (Ramírez-Chaves & Gómez-B., 2016): Publication type (Journal article, Conference proceedings, Book chapter, Book, Thesis, Conference paper); Relevance to the study (Main, Secondary); Anatomy and morphology; Taxonomy and Systematics; Biogeography; distribution and records; Threats and relationships with humans/Conservation (Threats, Conservation, Cultural aspects); Ecology and Natural History (Habitat use, Diet, Behavior, Abundance, Reproduction); Genetics, and Generalities (Compilation). Key words used for the searches included: *Coendou*, Colombia, *Sphiggurus* (a junior synonym of *Coendou*), *vestitus*.

Distribution

We reviewed specimens housed in Colombian museums and natural history collections including the Instituto de Investigaciones Biológicas Alexander von Humboldt, Villa de Leyva (IAvH), Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN), and Museo La Salle, Bogotá (MLS). Information on localities were obtained from specimen labels. In addition, we reviewed additional localities in the literature (e.g. Alberico et al., 1999; Voss, 2015; Ramírez-Chaves et al., 2016; Weksler et al., 2016). Of the examined specimens, but which were excluded in previous works, we took cranial measurements (Table 1) and compared them with those provided in the literature.

We also performed a SDM using Maxent version 3.4.0 (Phillips et al., 2017), which is a presence-background algorithm that compares occurrence localities based on environmental variables, with a sample of background pixels to create a prediction of suitability across the study area (Phillips et al., 2006, 2017; Phillips & Dudík, 2008). Maxent has been shown to outperform other algorithms, including when applied to small data sets (Elith et al., 2006; Pearson et al., 2007). We defined our study area creating a buffer around the localities (three confirmed localities, one dubious), which was calculated selecting the greatest distance among the localities based on Euclidian distances. We restricted this study area to ensure that Maxent select the bioclimatic data from ‘background’ pixels from a region in which known records are more likely to form a representative sample of the climatic conditions suitable for the species (Anderson & Raza, 2010; Peterson et al., 2011; Shcheglovitova & Anderson, 2013). To summarize environmental variation, we used 3 principal components (PCs) obtained from a Principal Component Analysis (PCA) for 19 bioclimatic variables (Hijmans et al., 2005). These PCs explained 88.5% of variance (PC1λ% 48.9, PC2λ% 25, PC3λ% 13.5) of the original variables. Since our sample sizes for the species was low, we used only the linear feature (see Phillips et al., 2006; Phillips & Dudík, 2008 for recommendations regarding sample sizes and features usage), and the default Maxent settings for other parameters were applied. To test the validity of the dubious locality, we built two models; one included the complete set of localities and another without the dubious locality. The area under the receiver operating curve (ROC), known as the AUC, was used to compare performance of the models. The AUC provides a single measure of model performance (Fielding & Bell, 1997) by giving the probability that the model correctly ranks a random presence site against a random absent site (Phillips et al. 2009). We excluded another model validation methodology due to the low number of localities available for *C. vestitus*.

Genetic characterization

To verify the taxonomic identity of one specimen (IAvH 7956), we extracted DNA from a sample of fresh tissue (labeled as IAvH 7940) that had been preserved in ethanol and stored at Colección de Tejidos del Instituto Alexander von Humboldt. For this purpose, we used the GeneJET Genomic DNA purification Kit (Thermo Scientific), following the manufacturer's recommendations. Almost the entire mitochondrial Cytochrome-*b* gene (CYTB) was amplified in two overlapping fragments of ~700 bp using the primers MVZ05 paired with PorcCytb676R, and PorcCytb565F paired with UMMZ04 (Voss et al., 2013). PCR programs consisted of a common initial denaturation of 94°C 2 min, and final extension of 72°C 6 min, for the two fragments, with 35 specific cycles of 94°C 30 s, 49°C 45 s, and 72°C 1 min. (fragment 1) and 94°C 30 s, 44°C 35 s, and 72°C 1 min (fragment 2). Amplifications of both fragments were carried out in a total volume of 50 µl, with about 1 µl of DNA, 1X buffer (with 2.0 mM of $MgCl_2$), 0.2 mM of dNTP's, 0.2 µM of each primer and 1.25 u/µl of DreamTaq DNA polymerase (Thermo Scientific). Sequencing of purified PCR products were performed in both directions with the amplification primers on an ABI 3500 sequencer (Applied Biosystems) at the "Servicio de Secuenciación y Análisis Molecular SSiGMol" at the Universidad Nacional de Colombia, Bogotá. We used Geneious R11 (Biomatters Limited) to edit and assemble overlapping sequences into a fragment of 1,121 bp that have been deposited in GenBank with accession number MG383643.

For comparative purposes, the Cyt-b sequence of IAvH 7956 was aligned with other erethizontid sequences downloaded from GenBank (genus *Erethizon* and *Coendou*) (Voss et al., 2013) using the MUSCLE algorithm as implemented in Geneious R11. The aligned sequence data were analyzed using Bayesian inference

(BI) in Mr Bayes 3.2.6 (Ronquist et al., 2012): we determined the best fitting model of sequence evolution in jModelTest 2.1.10 (Darriba et al., 2012), under the Akaike Information Criterion (AIC). The best model was GTR+G, with gamma distribution (0.2130) and base frequencies A=0.3246, C=0.2901 G=0.0946 T=0.2908. It was implemented in the running of two independent Markov Chain Monte Carlo (MCMC) analyses for 2 X 10^7 generations, sampling every 20,000 generations. The 25% of trees from each run were discarded as burn-in and the remaining (15,000 trees) were combined to estimate tree topology, mean likelihood and posterior probabilities. We considered that a node received strong (significant) support when its posterior probability was ≥ 0.95, and negligible (non-significant) support when it was < 0.95 (Gutiérrez et al., 2014).

Finally, the mean pairwise genetic distances of our matrix were estimated in MEGA 7 (Kumar et al., 2015) using the Kimura 2-parameter model of evolution (Kimura, 1980), and then compared with typical intra and inter-specific values reported for different rodents (Bradley & Baker, 2001), and specifically for porcupines (Voss et al., 2013).

Rarity and threat category

To evaluate the rarity of the species, we followed the criteria of Yu & Dobson (2000) that used four characteristics (local population density, the area of the species range, the number of different kinds of habitats that the species occupies, and body size), and suggested tentative factors that might determine the rarity category of this species. We also compared the number of records for the species in Colombia and compared the area of distribution (in terms of AOO and EOO), to determine if the species is among the rarest porcupines in the country.

We used the information on distribution and rarity to explore whether they can be applied to the definition of threatened categories following the criteria of the International Union for Conservation of Nature - IUCN (IUCN, 2012). Additionally, we estimated the Extent of occurrence (EOO) calculating the convex minimum polygon, and the Area of occupancy (AOO) summing the area of square grids the species occupies in GeoCAT (http://geocat.kew.org; Bachman et al., 2011), drawn around the range polygons with the data of the confirmed localities (IUCN, 2012).

Results

State of knowledge

We found 14 published documents related with *C. vestitus*. Of these, seven were journal articles (Thomas, 1899; Tate, 1935; Alberico et al., 1999; Voss & da Silva, 2001; Alberico & Moreno, 2006; Voss, 2011; Voss et al., 2013; Ramírez-Chaves et al., 2016), six were part of books or book chapters (Cabrera, 1961; Honacki et al., 1982; Eisenberg, 1989; Emmons & Feer, 1997; Alberico & Moreno, 2006; Voss, 2015), and one was an online publication (Weksler et al., 2016). More recurrent research topics were “Taxonomy and Systematics”, and “Biogeography, distribution and records” with 11 publications, followed by “Anatomy and morphology” with seven studies. Only two studies were included in “Threats and relationships with humans/Conservation”. Only one study (Voss et al., 2013) provided genetic information on the species. We found no studies in the additional topics evaluated (i.e. Ecology and Natural History).

Distribution

Based on voucher specimens housed in Colombian collections, and information from the literature, *C. vestitus* is found in four localities in the Eastern

Cordillera of Colombia, but one is doubious. The first locality was in Department of Cundinamarca, San Juan de Río Seco (4°51'4"N – 74°38'1"W; 1,440 m), which is based on one specimen (MLS 248) collected in March 1924, and six more specimens collected between 1923 and 1925, housed at the American Museum of Natural History, New York (AMNH), Natural History Museum, London (BMNH), the Muséum National d'Histoire Naturelle, Paris (MNHN), and the National Museum of Natural History, Washington, D.C. (USNM; Voss & da Silva, 2001). The second locality is Quilipe, Cundinamarca (4°44'50"N – 74°31'59"W; 1,250 m), based on a female specimen housed at the AMNH (AMNH 70529) collected in 1925. The third locality (a doubious one) is Meta, Villavicencio (4°10'0"N – 73°39'0"W; ~610 m), which is supported by one female specimen (ICN 3505), without additional data, and obtained in a market place called Siete de Agosto. The fourth locality is the Department of Boyacá, Villa de Leyva, vereda Llano del Árbol (5°37'59"N – 73°31'32"W; 2,070 m), which is based on a female specimen (IAvH 7956/MLS 753; Fig. 1), collected on 21 September 2005. IAvH 7956/MLS 753 has not been included in previous works, and matches the diagnostic characters suggested for the species: small size (weight 865 g), tail very short (less than 50% of head and body length); dorsal pelage with long blackish fur that partially or completely conceals defensive quills; bristle-quills bicolored. Diagnostic cranial characters include a bony palate between the toothrows marked by a high median keel flanked by deep lateral grooves, and alisphenoid incompletely ossified (Voss & da Silva, 2001; Voss, 2015). The coronoid process is present but not developed, and the mesopterygoid fossa extends anteriorly until the posterior part of the M2 (Fig. 1). Cranial and external measurements are within the known ranges for the species, except for the length of tail, length of the hindfoot, condylo-incisive length, breadth of M1, posterior zygomatic breadth, and breadth of braincase, all of wich are slightly smaller (Table 1).

The most important variables to describe the bioclimatic conditions for the species were: Annual Mean Temperature, Maximum Temperature of Warmest Month, Minimum Temperature of Coldest Month, Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Mean Temperature of Warmest Quarter, Mean Temperature of Coldest Quarter, Isothermality, Precipitation of Driest Month, Precipitation of Driest Quarter and Precipitation of Warmest Quarter (Supplementary Table S1). The model built without the dubious locality showed strong differences in AUC $_{\text{training data}}$ (0.951) (Fig. 2A) and it was therefore superior to the one from the complete data set (AUC $_{\text{training data}}$ =0.641) (Fig. 2B). Model 1 (Fig. 2A) indicated a zone with higher suitability values in the Eastern Cordillera, while model 2 extrapolated the climatic conditions suitable for the species to the Central Cordillera (Fig. 2B). Additionally, model 1 showed a higher maximum suitability value (0.72) than model 2 (0.52). The bioclimatic environment corresponding to the dubious locality differed from those corresponding to the rest of records (Fig. 3), and it represents extreme conditions in the climatic conditions: Annual Mean Temperature and Annual Precipitation relationship (Fig. 3D).

Genetic characterization

The patterns of relationships we recovered in our Cyt-b tree are almost identical to those presented by Voss et al. (2013), using Maximum Parsimony and Maximum Likelihood, but Bayesian Inference provides additional support for the monophyly of *Coendou* and other nodes (Fig. 4). The specimen we sequenced (IAvH 7956, from Villa de Leyva, Boyacá) appears as the sister taxon of the specimen AMNH 70596 in Voss et al. (2013), collected in San Juan de Río Seco, at the

Department of Cundinamarca. Both are consistent with a monophyletic group with strong support, thus confirming the taxonomic identity of IAvH 7956 as *Coendou vestitus*.

The Cyt-b sequence we obtained from IAvH 7940 constitutes the second and most complete (almost the entire coding region) molecular record of the species, and a new haplotype with an average genetic distance of 1.2% from AMNH 7056 (Voss et al., 2013). This value is within the range of previously reported intraspecific variation in *Coendou* and other rodents (Bradley & Baker, 2001; Voss et al., 2013).

Also, we found better-supported sister relationship between *C. vestitus* and *C. pruinosus* (parapatric species) and their membership to a larger clade along with *C. ichillus* and *C. melanurus* (Fig. 4). The interspecific genetic distances between the specimen IAvH 7940 and other *Coendou* species ranges from 3.6% with *C. pruinosus* (its sister taxon) to 13% with *C. nycthemera.*

Rarity and threatened category

Coendou vestitus matches the criteria of an extremely rare species (Category H; Yu & Dobson, 2000), considering that this species is rare in all three factors: a reduced distribution (EOO 1,195 km^2; AOO 12 km^2: 2 km cell size), low population based on the scarcity of records in the last 100 years, and the lower number of different kinds of habitats occupied (tropical moist broadleaf forest; Olson et al., 2001) located in the highly threatened sub-Andean and Andean forests. The adult body size of *C. vestitus* (length of head and body about 330 – 370 mm), is within the size range observed for small *Coendou* species.

In addition, using only three validated localities (see discussion), the estimated EOO 1,195 km^2 and AOO 12 km^2, are associated with the humid sub-montane forest, which in the case of Colombia is an ecosystem that has been significantly degraded. The species likely has low population density due to the few confirmed records. With this information, we suggest that the species should be better classified as Endangered (EN) following the IUCN (2012) criteria, based on three factors: 1) Restricted distribution with AOO less than 500 km^2; 2) Habitat fragmentation and degradation, and 3) Estimated reduction of the population.

Discussion

Our results showed that *C. vestitus* is one the least studied species of the genus in Colombia, and is in urgent need of further field studies to understand aspects of its natural history, ecology, conservation and distribution. It is known from the Andes, the ecosystem with high rates of degradation and fragmentation (Thiollay, 1996) where most of the historical biological expeditions have occurred, it is only known from three definitive localities, one dubious locality and only 13 specimens (three without precise locality data). Most of the information on natural history and ecology is based on inference, rather than observations (e.g. Alberico & Moreno, 2006; Weksler et al., 2016). The most recent record (IAvH 7956/MLS 753) was kept in captivity for three weeks, as noted on the voucher label. Furthermore, it is the only porcupine species included in a threatened category in Colombia (VU: Alberico & Moreno, 2006; MADT, 2014), although globally any species of *Coendou* are listed as threaten (IUCN, 2017).

Distribution

The elevational distribution of the *C. vestitus* has been suggested as ranging from 1,300 to 2,600 m (Barthelmess, 2016), 250 to 2,000 m (Alberico et al., 1999), and 600 to 1,440 m (Ramírez-Chaves et al., 2016). Based on the information of confirmed localities, and discarding the dubious record from Villavicencio, the updated elevational range is from 1,250 (Cundinamarca, Quilipe) to 2,070 m (Boyacá, Villa de Leyva). Furthermore, our model confirms that *C. vestitus* has an area of distribution restricted to the Central Colombia Cordillera, a region characterized by the presence of tropical dry forests and the montane ecosystems of the western slopes of the Eastern Cordillera of Colombia. The geographic map and the environmental space (PCA) provides evidence against the validity of the locality in Villavicencio, from which the voucher (ICN 3505) is based on a specimen bought in a local market and brought there from another unknown locality (Alberico & Moreno, 2006).

Genetic data

Although most of the species in the genus *Coendou* have been characterized for at least one molecular marker, in comparison with other neotropical mammalian/rodent groups, porcupines have received less attention from the perspective of genetics and molecular phylogenetics. This is in part due to the rarity and scarcity of recent collections of many species, as in the case of *C. vestitus*. Evidence of that can be found in the most complete work about those topics, in which the genetic data (CytB) from “rare” species were recovered from museum skins collected several years ago (Voss et al., 2013). Particularly for Colombia, there are only CytB sequences in GenBank from 4 of the 7 species reported (Ramírez-Chaves et al., 2015), one of them being *C. vestitus*. The only haplotype of this species available until now (682 bp) was obtained from the skin of a specimen deposited in the American Museum of Natural History and collected in the 1920s. The new haplotype we report here (1123 bp) constitutes advance towards the genetic characterization of large rodents in the country. Furthermore, as pointed by Ramírez-Chaves et al. (2016), the molecular information, as well the morphological, are essential to resolve basic aspects of the taxonomy and species distribution of neotropical porcupines, this is a first step in the process of conservation, especially of rare taxa such as *C. vestitus*.

Rarity and threat category

Because of the scarcity of records, *C. vestitus* is considered a rare species. Although other porcupines are known from fewer specimens in Colombia (e.g. *C. ichillus*), they are also distributed in other countries (see Voss, 2015), whereas *C. vestitus* is endemic to a small area in the Andes of Colombia (Ramírez-Chaves et al., 2016). The rarity is also attributed to its reduced distribution and the few habitat types that it apparently inhabits (only one according to our model). In general, small-sized species of *Coendou* (e.g. *C. ichillus*, *C. roosmalenorum*) have more restricted distributions in the northern part of South America, compared with the larger species which have only one type of hair (quills) in adulthood (e.g. *C. prehensilis* and *C. bicolor,* with 400–530 mm of length of head and tail approximately; Voss, 2015). It is possible that the rarity of this taxon is associated with these functional attributes such as the presence of three types of hairs in adulthood and small size, although these characters have evolved homoplasiously (Voss et al., 2013). Perhaps, the differences in the trophic-niche shift (Voss et al., 2013) have an influence in the distribution area, or evidently, having mostly quills in adulthood provide an extreme advantage against predators. Other morphological characters (as the presence of swollen nasofrontal sinuses and larger tails, as observed in *C. bicolor* and *C. prehensilis*), or a combination of them, may confer an adaptive advantage (Voss et al., 2013). However, the ecomorphological or evolutionary reasons behind the restricted distributions of small–sized *Coendou* are not clear yet, and this topic needs further research. In addition, considering that rodents have relatively low frequencies of rare species (Ceballos & Brown, 1995; IUCN, 1997), that *C. vestitus* is in the highest degree of rarity and confirmed records are not in any protected area, research activities should be a priority for this taxon.

Based on the extent of distribution and rarity, we suggest the transference of the current threaten category (DD) to Endangered (EN) based on three factors: 1) Restricted distribution with AOO less than 500 km^2; 2) Habitat fragmentation and degradation, and 3) Estimated reduction of the population because the scarcity of recent records. The small distribution size can be an indication of the risk of extinction, being the most frequently used criteria in the IUCN (2012) to evaluate threat categories (Gaston & Fuller, 2008). Therefore, the threat category corresponds to the criteria B1 and B2 (EOO <5,000 km^2, AOO <500 km^2, <5 locations, continuous decrease). This conclusion is justified by the IUCN criteria, which mention that poorly known taxa can be assessed in a threaten category based on information inferred of habitat loss and restricted distribution, and therefore avoid assigned them a DD category which can be put in a higher risk the taxon. In addition, our analyses provide potential distribution maps, which could be used to guide field surveys and thus to accelerate the discovery of unknown populations of *C. vestitus*, especially if these surveys are planned to be conducted in the areas of high probability of occurrence of this species.

Acknowledgements

We thank Hugo López (ICN), Cristian Cruz Rodríguez (MLS) for allowing to review specimens under their care. Luiz H. Varzinczak provided useful comments on an early version of the manuscript. MMTM thanks to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes, Brazil) for support. Thanks to the Posgrado en Ciencias Biológicas, UNAM and the National Council for Science and Technology (CONACYT), Mexico for providing funding and facilities to EANU to develop Doctoral studies at UNAM (scholarship 290840). HERC thanks to IAvH (Andrés M. Cuervo and María López Rodríguez) for access to the tissues analyzed in this document, and to Rufford Small Grants (Grant 23710-1) for support.

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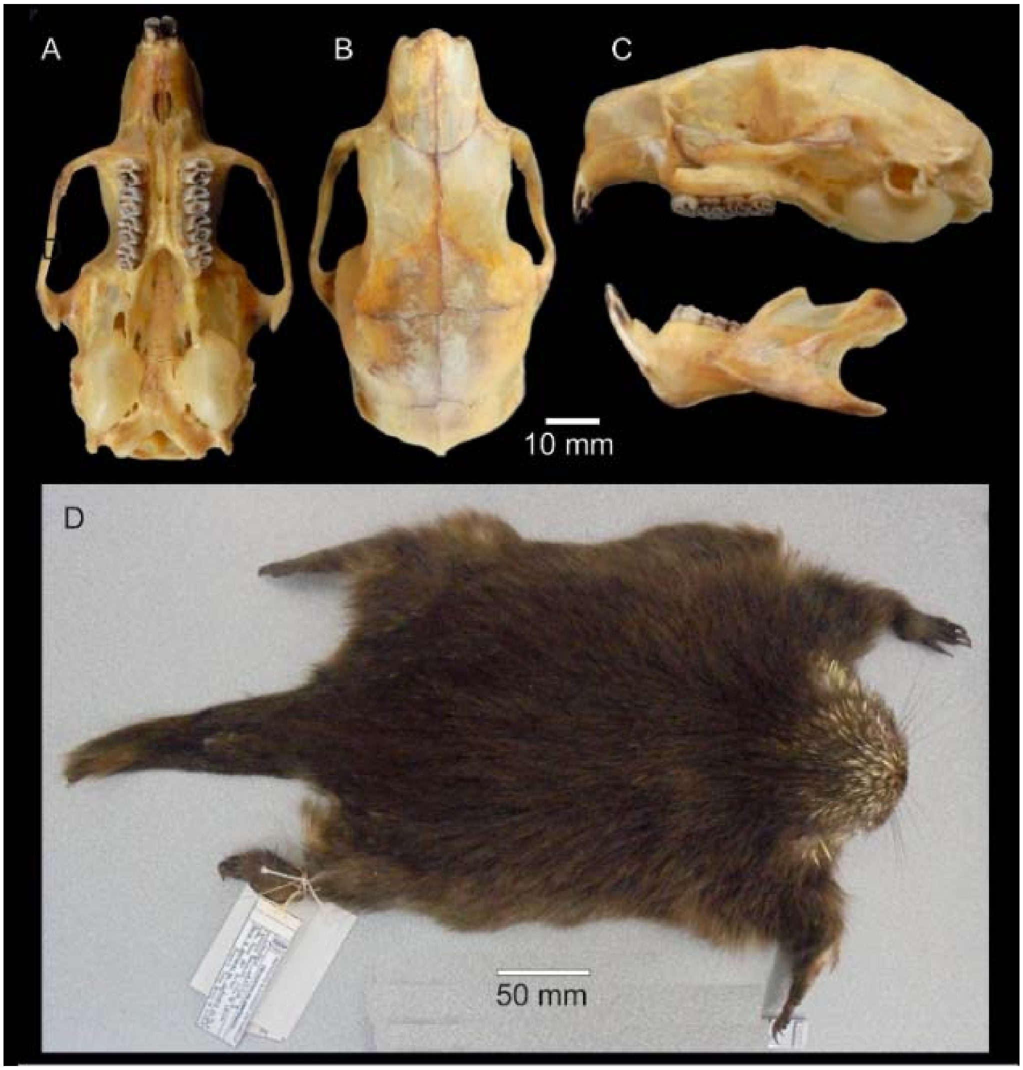

Figure 1. *Coendou vestitus* (IAvH 7956/MLS 753) from Villa de Leyva, Colombia. This specimen has not been illustrated in previous accounts. Details of the skull (A. Ventral view, B. Dorsal view, C. Lateral view) and the skin (D).

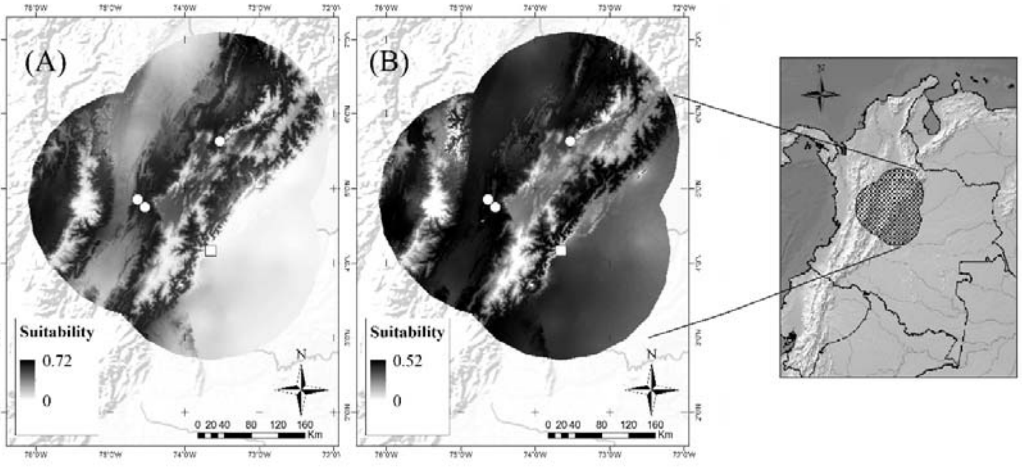

Figure 2. Projections of Maxent models onto the Central Colombia, showing categorical estimates of the climatic conditions suitable for the *C. vestitus*. (A) Prediction obtained from the model built with the three confirmed localities (without one dubious locality). (B) Prediction obtained from the model built with the complete set of localities (three confirmed localities plus one dubious locality). Black Lines indicate contours of study area. Dark color: areas of higher values of suitability. Symbols indicate localities of the studied species, with circles marking those confirmed localities and square marking the dubious locality.

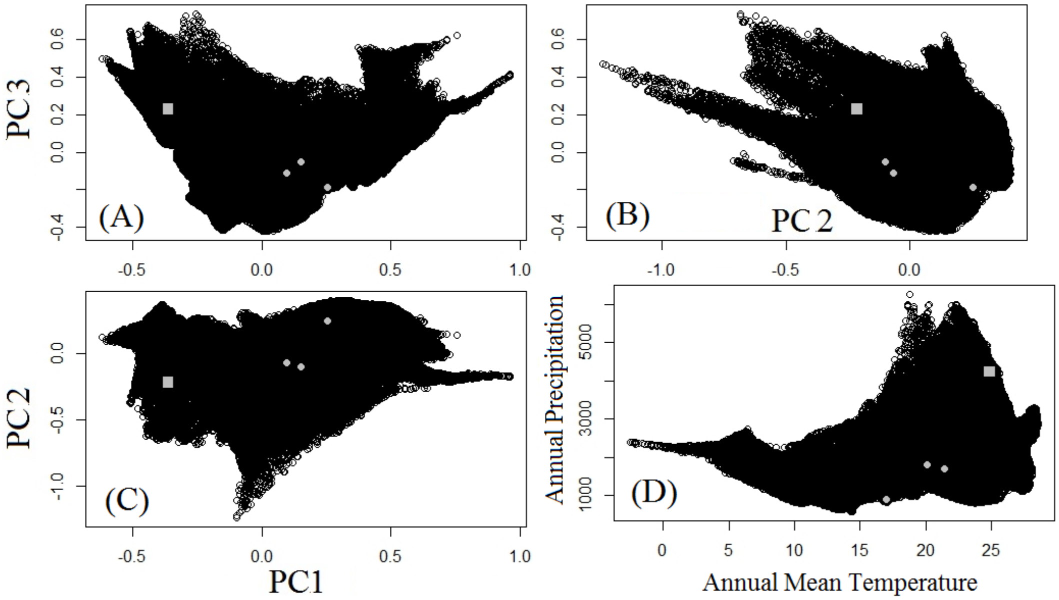

Figure 3. Environmental plots represented by relationship between three Principal components (PC1 88.3%, PC2 9.8%, PC 3.8% of variance) from 19 Bioclimatic variables. (A) Relationship between PC1 vs PC3. (B) Relationship between PC2 vs PC3. (C) Relationship between PC1 vs PC2; and (D) Relationship between Annual Mean Temperature vs Annual Precipitation. Symbols indicate localities of the studied species in the environmental cloud obtained from the PCs pixels across the study area, with circles marking those confirmed localities and square marking the dubious locality.

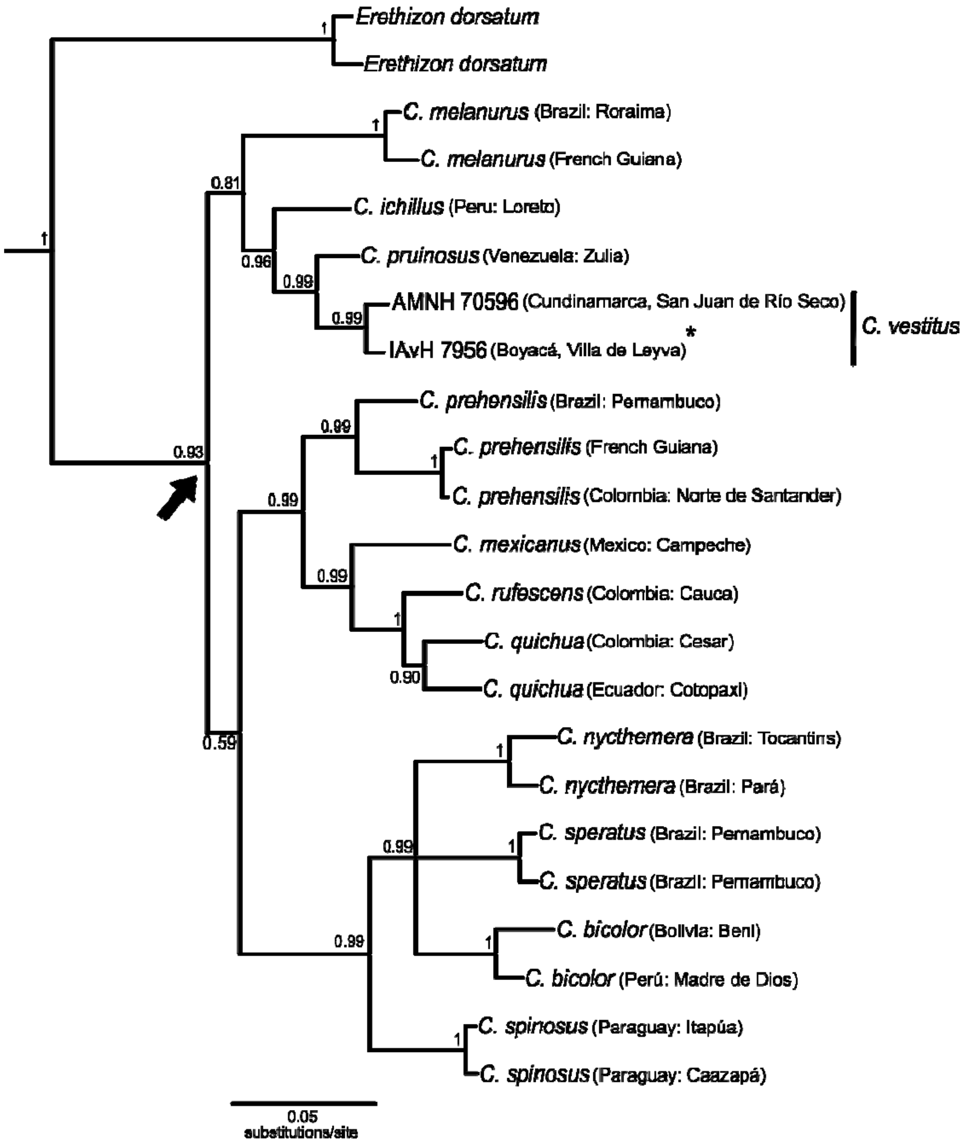

Figure 4. Bayesian CytB tree of *Coendou,* with the black arrow pointing the ancestral node of the genus. Specimens are identified by country of origin and next largest political unit, except the two specimens of *C. vestitus* from Colombia that are identified by collection number and collection locality. The new record for the species presented here is highlighted by an asterisk. Nodal support values are posterior probabilities.

Table 1. External and cranial measurements of *Coendou vestitus*. Information of IAvH 7956/MLS 753 has not been included in previous reviews. Measurements include the mean, the observed range in parentheses, and the sample size of specimens housed at the AMNH, BMNH, MNHN, and USNM (Voss and Da Silva 2001). For the holotype, the MTR one or both endpoints include dP4 instead of P4. See text for Museum abbreviations.

	BMNH 54.6.26.1 Holotype Subadult	**Adults**	**IAvH 7956/MLS 753**
Sex	Unknown	5 females, 3 unknown	Female
Head-and-body length (HBL)	-	346 (330-370) 6	287 approx.
Length of tail (LT)	-	179 (170-195) 6	163
Length of the hindfoot (HF)	57	60 (56-63) 6	52.6
Condylo-incisive Length (CIL)	-	66.8 (65.4-68.3) 6	63.4
Length of Diastema (LD)	[15.2]	17.4 (16.9-17.9) 7	15.3
Length of Incisive Foramen (LIF)	3.9	4.2 (3.6-4.9) 7	3.88
Breadth of Incisive Foramina (BIF)	2.5	2.9 (2.7-3.1) 7	2.79
Maxillary Tooth Row (MTR)	[14.8]	15.5 (14.7-16.4) 7	15.7
Length of Molars (LM)	11.3	11.3 (10.8-12.0) 7	11.7
Breadth of P4 (BP4 [dP4])	[3.6]	4.5 (4.1-4.9) 7	4.4
Breadth of M1 (BM1)	3.8	4.0 (3.8-4.3) 7	3.7
Anterior Palatal Breadth (APB)	4.1	4.9 (4.2-5.6) 7	4.5
Posterior Palatal Breadth (PPB)	5.5	6.2 (5.1-7.2) 7	6.3
Posterior Zygomatic Breadth (PZB)	40.3	42.9 (42.1-43.5) 6	39.9
Height of the Infraorbital	8.0	10.4 (9.8-11.0) 7	9.3

Foramen (HIF)			
Zygomatic Length (ZL)	24.9	27.2 (26.2-28.1) 7	26.3
Length of Nasals (LN)	18.6	20.2 (18.9-21.8) 5	19.8
Breadth of Nasal Aperture (BNA)	9.0	10.7 (10.4-11.2) 7	9.5
Breadth of Braincase (BB)	29.1	29.8 (27.8-30.6) 7	26.8
Depth of Incisor (DI)	3.1	3.3 (3.1-3.5) 7	3.4
Breadth of the Incisor Tips (BIT)	4.1	4.6 (4.2-4.8) 7	6.0

Supplementary Material

Supplementary Table S1. Loading factors of the bioclimatic variables used in the principal component analysis. PC= Number of principal components from PCA.

Variable	C1	C2	C3
BIO1 = Annual Mean Temperature	**0.307**	**0.046**	**0.181**
BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))	**0.124**	**.036**	**0.293**
BIO3 = Isothermality (BIO2/BIO7) (* 100)	**.082**	**0.350**	**0.281**
BIO4 = Temperature Seasonality (standard deviation *100)	**0.209**	**.252**	**.231**
BIO5 = Max Temperature of Warmest Month	**0.312**	**0.008**	**0.167**
BIO6 = Min Temperature of Coldest Month	**0.304**	**0.061**	**0.170**
BIO7 = Temperature Annual Range (BIO5-BIO6)	**0.159**	**.265**	**0.045**
BIO8 = Mean Temperature of Wettest Quarter	**0.304**	**0.053**	**0.197**
BIO9 = Mean Temperature of Driest Quarter	**0.310**	**0.036**	**0.167**
BIO10 = Mean Temperature of Warmest Quarter	**0.310**	**0.030**	**0.163**
BIO11 = Mean Temperature of Coldest Quarter	**0.303**	**0.059**	**0.196**
BIO12 = Annual Precipitation	**0.207**	**0.241**	**.333**
BIO13 = Precipitation of Wettest Month	**0.224**	**0.187**	**.342**
BIO14 = Precipitation of Driest Month	**.067**	**0.422**	**0.076**
BIO15 = Precipitation Seasonality (Coefficient of Variation)	**0.186**	**.286**	**.215**
BIO16 = Precipitation of Wettest Quarter	**0.228**	**0.153**	**.379**
BIO17 = Precipitation of Driest Quarter	**.011**	**0.440**	**0.010**
BIO18 = Precipitation of Warmest Quarter	**.098**	**0.370**	**.082**
BIO19 = Precipitation of Coldest Quarter	**0.233**	**0.147**	**.358**

IV

CHAPTER II

The distribution of the Brazilian porcupine *Coendou prehensilis* (Erethizontidae) in Colombia: Confirmation of its occurrence in the Colombian Amazon and an update

The distribution of the Brazilian porcupine *Coendou prehensilis* (Erethizontidae) in Colombia: Confirmation of its occurrence in the Colombian Amazon and an update

Abstract

The Brazilian porcupine *Coendou prehensilis* is distributed from northwestern South America to northeastern Paraguay and northwestern Argentina. In Colombia, it is present mainly in the Caribbean, the Eastern plains and the Andean regions, which correspond to six of the biogeographical provinces of the country. Its presence in the Colombian Amazon region has been suggested based on records from neighboring countries such as Ecuador, Venezuela and Brazil. However, no voucher specimens or additional evidence that corroborates the presence of the species in that region of Colombia is known. Based on the review of specimens deposited in Colombian collections, analyses of photographic records, and literature, the presence of the species in the Colombian Amazon is confirmed, and its distribution in the country updated. Overall, we found 35 records of *C. prehensilis* in Colombia, of which seven corresponds to the Colombian Amazon (four photographic records and three specimens). A genetic analysis based on cytochrome-b suggests this species as genetically uniform throughout its distributional range. These new records make *C. prehensilis* the species of the genus that inhabits the largest number of natural regions and biogeographic provinces of Colombia, whereas other species of *Coendou* are restricted to one or two provinces.

Resumen

Distribución del puercoespín arborícola *Coendou prehensilis* (Erethizontidae) en Colombia. El puercoespín arborícola *Coendou prehensilis* se distribuye desde el noroccidente de Suramérica hasta el noreste de Argentina y noroeste de Paraguay. En Colombia se ha registrado principalmente en el Caribe, los Llanos orientales y los Andes, que corresponden a seis de las provincias biogeográficas del país. Se ha sugerido su presencia en la región Amazónica colombiana con base en registros de países limítrofes como Ecuador, Venezuela y Brasil. Sin embargo, no se conocen ejemplares testigo o evidencia adicional que corroboren la presencia de la especie en dicha región de Colombia. A partir de la revisión de ejemplares depositados en colecciones colombianas, el análisis de registros fotográficos y de literatura confirmamos la presencia de la especie en la Amazonía colombiana y actualizamos la distribución de la especie en el país. En general, encontramos 35 registros de *C. prehensilis* en Colombia, de los cuales siete corresponden a la Amazonía colombiana (cuatro registros fotográficos y tres especímenes). El análisis genético basado en citrocromo-b sugiere esta especie es genéticamente uniforme en todo su rango de distribución. Los nuevos registros convierten a *C. prehensilis* en la especie del género que más regiones naturales y provincias biogeográficas habita en Colombia, mientras que otras especies se restringen a una o dos provincias.

Keywords: Amazon. Biological collections. Biogeographic provinces. Cytochrome-b. Porcupine.

Palabras clave: Amazonas. Citocromo-b. Colecciones biológicas. Provincias biogeográficas. Puercoespín.

Introduction

The genus *Coendou* is distributed in tropical and subtropical forests from Mexico to Uruguay, and comprises between 13 and 15 species for the America (Voss 2015; Barthelmess 2016). Among them, the Brazilian porcupine *Coendou prehensilis* presents the widest distribution: from northeastern South America, in Colombia, Venezuela and the Guianas, to northwestern Argentina and eastern Paraguay, through countries such as Ecuador, Peru, Brazil and eastern Bolivia (Voss 2011; 2015). In spite of being a widespread species, the limits of its current distribution are still unknown (Leite et al. 2011).

In Colombia, *C. prehensilis* has been confirmed in six biogeographic provinces (Hernández Camacho et al. 1992), in the departments of Magdalena (Sierra Nevada de Santa Marta Province), Atlántico, Cesar, Sucre (Peri-Caribbean arid belt Province), Córdoba (inter-Andean zone of the Magdalena River of the Chocó-Magdalena Province), Norte de Santander and Cundinamarca (North Andean Province), Meta and Vichada (Orinoquía Province), and Guaviare (Guyana Province) (Racero-Casarrubia et al. 2016; Ramírez-Chaves et al. 2016). In addition, the potential presence of the species in the Colombian Amazon has been suggested from records in the Ecuadorian (Pastaza), Venezuelan (San Juan Manapiare), Brazilian (Villa Bella Imperatriz) and Peruvian (Huampami) Amazon (Voss 2011; Paglia et al. 2012; de Freitas et al. 2013; Ramírez-Chaves et al. 2016). Despite that, there are not confirmed records that validate the presence of the species in this region of Colombia.

In general, the Brazilian porcupine is currently considered the species of *Coendou* with the widest distribution in Colombia, however there are still gaps on information about its current distribution, and its the presence in some national provinces is still doubtful. Furthermore, the populations of the Caribbean region of the country have been considered as an endemic different taxon (*Coendou sanctaemartae*; see Alberico et al. 1999; Solari et al. 2013), and some melanic individuals were misidentified as *C. bicolor* (Ramírez-Chaves et al. 2016). Here we confirm the presence of *C. prehensilis* in the Colombian Amazon. Additionaly, we present new data on the presence of *C. prehensilis* in the Colombian Amazon and provide a new cytochrome-b sequence of one individual from northern Colombia, updating its distribution in the country. We also discuss the validity of *C. sanctaemartae*. For this, we reviewed vouchers housed at national collections not included in previous reviews of the genus (e.g. Alberico et al. 1999; Ramírez-Chaves et al. 2016), and evaluated photographic and bibliographic records.

Materials and methods

We examined specimens deposited at Museo de La Salle (MLS), Bogotá; Universidad Distrital Francisco José de Caldas (MUD), Bogotá; Instituto de Ciencias Naturales de la Universidad Nacional de Colombia (ICN), Bogotá; Colección de Mamíferos, Universidad de Caldas (MHNUCa), Manizales; and Colección de Mamíferos del Museo Javeriano de Historia Natural “Lorenzo Uribe Uribe” (MPUJ), Bogotá. To corroborate the identification of the specimens, we used cranial and external characters available in literature (e.g. Voss 2011; 2015; Ramírez-Chaves et al. 2016). For this, the following cranial measurements (in millimeters) were taken from adult specimens: condyle-incisive length (CIL), length of diastema (LD), length of maxillary tooth row (MTR), length of molars (LM), breadth of P4 (BP4), breadth of M1 (BM1), anterior palatal breadth (APB), posterior palatal breadth (PPB), posterior zygomatic breadth (PZB), height of the infraorbital foramen (HIF), zygomatic length

(ZL), length of nasals (LN), length of nasals (BNA), breadth of braincase (BB), depth of incisor (DI), and breadth of the incisor tips (BIT).

In addition, we analyzed three photographic records from the Colombian Amazon, and one from the Caribbean and Orinoco regions. Also, we reviewed a video of a specimen recorded as *Coendou melanurus* in literature (Acevedo-Quintero & Zamora-Abrego 2016), and additional bibliographic information (Negret et al. 2015; Racero-Casarrubia et al. 2016). We used all these records to update the distribution of the species in the country.

Furthermore, we performed the genetic characterization of one specimen housed at the Colección de Mamíferos of the Instituto Alexander von Humboldt (IAvH 6786). The specimen (IAvH 6786) was collected in 1999 in vereda El Diamante, north-eastern sector of Parque Nacional Natural Tamá, Toledo, Norte de Santander (07°7'19.6"N – 72°14'0.01"W). The locality is central to the populations historically allocated to *C. prehensilis* and *C. sanctaemartae* in Colombia. We extracted DNA from a sample of fresh tissue preserved in ethanol (labeled as IAvH 123), and stored at Colección de Tejidos of the Instituto Alexander von Humboldt. For this purpose, we used the GeneJET Genomic DNA purification Kit (Thermo Scientific), following the manufacturer's recommendations. We amplified the entire mitochondrial cytochrome-b gene (cyt-b) in two overlapping fragments of ~700 bp using the primers MVZ05 paired with PorcCytb676R, and PorcCytb565F paired with UMMZ04 (Voss et al. 2013). PCR programs consisted of a common initial denaturation of 94°C 2min., and final extension of 72°C 6 min., for the two fragments, with 35 specific cycles of 94°C 30 sec., 49°C 45° sec., and 72°C 1 min. (fragment 1) and 94°C 30 sec., 44°C 35 sec. And 72°C 1 min. (fragment 2). We carried out amplifications of both fragments in a total volume of 50 µl, with about 1 µl of DNA, 1X buffer (with 2.0 mM of $MgCl_2$), 0.2 mM of dNTP's, 0,2 µM of each primer and 1.25 u/µl of DreamTaq DNA polymerase (Thermo Scientific). Sequencing of purified PCR products was performed in both directions with the amplification primers on an ABI 3500 sequencer (Applied Biosystems) at the "Servicio de Secuenciación y Análisis Molecular SSiGMol" at the Universidad Nacional de Colombia. We used Geneious R11 (Biomatters Limited) to edit and assemble overlapping sequences into a fragment of 1140 bp that have been deposited in GenBank with accession number MG775435.

For comparative purposes, we aligned the cyt-b sequence of IAvH 6787 with other erethizontid sequences downloaded from GenBank (genus *Erethizon* and *Coendou*; Voss et al. 2013) using the MUSCLE algorithm as implemented in Geneious R11. We analyzed the aligned sequence data using Bayesian inference (BI) in MrBayes 3.2.6 (Ronquist et al. 2012). For this, we determined the best fitting model of sequence evolution in jModelTest 2.1.10 (Darriba et al. 2012), under the Akaike Information Criterion (AIC), and implemented the running of two independent Markov Chain Monte Carlo (MCMC) analyses for 2×10^7 generations, sampling every 20.000 generations. The first 25% of trees from each run were discarded as burn-in and the remaining (5,000 trees) were combined to estimate tree topology, mean likelihood and posterior probabilities. We considered that a node received strong (significant) support when its posterior probability was ≥ 0.95, and negligible (non-significant) support when it was < 0.95 (Gutiérrez et al. 2014).

Finally, we estimated the Mean pairwise genetic distances of our matrix in MEGA 7 (Kumar et al. 2015) using the Kimura 2-parameter model of evolution (Kimura 1980), and then they were compared with typical intra and inter-specific values reported for different rodents (Bradley & Baker 2001), and specifically for porcupines (Voss et al. 2013).

Results

Based on our review of collection, photographic, and literature records, *C. prehensilis* is present in 35 localities from 24 municipalities in Colombia, in the departments of Amazonas, Antioquia, Atlántico, Casanare, Caquetá, Cesar, Córdoba, Guaviare, Meta, Norte de Santander, Putumayo, Sucre, and Vichada. These localities belong to the biogeographical provinces of Amazonia, North Andean, Orinoco, Peri-Caribbean arid belt and Sierra Nevada de Santa Marta (Fig. 1).

Confirmation of the presence of *C. prehensilis* in the Colombian Amazon: We found one female *C. prehensilis* preserved as skin and skull (MLS 1093). It was collected in 1950, municipality of Florencia, Caquetá (1°36′51″N - 75°36′42″W; ~242 m), Colombian Amazon. MLS 1093 presents the diagnostic morphological characteristics for the species (Voss 2011; 2015; Fig. 2). Among these are the presence of bi-colored (white or yellowish-whitish at the base and black at the tip) and tri-colored (bright yellow at the base, black in the middle and whitish-yellow at the distal portion) spines; cranially, it have the frontal sinuses inflated, wide nasal aperture and the upper incisors are distinctively procumbent (de Freitas 2013 et al.; Leite et al. 2011; Voss 2011; 2015). The cranial measurements of MLS 1093 are in accordance with those recorded for other specimens from Colombia (Table 1; Ramírez-Chaves et al. 2016).

Coendou prehensilis was also recorded from El Caraño, km 20 via Florencia-Neiva (1°43'54.07"N - 75°40'39.93"W; ~240 m), Department of Caquetá, based on a specimen found dead on April 8, 2015 (ICN 23137). The cranium and spines observed (Fig. 3) present the diagnostic characteristics of the species. At the morphometric level, the skull showed the known intervals for the species in Colombia (Table 1).

In addition, we reviewed a juvenile specimen (ICN 21151), preserved in alcohol, from the Serranía El Churumbelo (1°14′32"N - 76°30′28"W; ~400 m), Mocoa, Department of Putumayo, previously identified as *Coendou* sp. (Ramírez-Chaves et al. 2013). ICN 21151 exhibits soft hair characteristic of immature individuals (Voss & Da Silva 2001). Although the identification of ICN 21151 is complex because it is not possible to observe diagnostic characters, it is tentatively assigned to *C. prehensilis* because of its size (too large to be a juvenile of other Amazonian species recorded in Colombia), the brownish fur coloration (observed in juveniles of *C. prehensilis*), and its distribution. Additionally, one specimen from Natural Reserve “Bojonawi”, Vichada (MUD 566; 6° 6'8.10"N - 67°29'26.30"W; ~50 m) confirms the presence of the species in the limits of the Orinoco and Amazon basins.

From photographs, the species is recorded in four localities from the Colombian Amazon region: 1) Puerto Alegría (1°00′20″S - 74°00′54″W; 120 m), Amazonas, based on an individual photographed in January 2016, which was captured and kept in captivity in the aforementioned locality; 2) Leticia, headquarters of the Universidad Nacional de Colombia (4°11′37″S - 69°56′27″W; ~95 m), Amazonas; 3) Belén de Los Andaquíes (1°24'37.20"N - 75°53'55.37"W; ~320 m), in the road to the Ecotourism Reserve "El Horeb", Caquetá; 4) San José del Guaviare in proximity to the “La María” Lake (02º31′42.26″N - 72º41′27.38″W; 210 m), Guaviare.

We also reviewed a literature record identified as *C. melanurus,* which was reported in a study carried out 3.5 km from the biological station "El Zafire" in the Colombian Amazon (3°56’48’N - 69°53’11’W; 80 m; Acevedo-Quintero & Zamora-Abrego 2015). The record is based on a video in which a large individual is observed, with only one type of spine present and the anterior part of the nostrils located above the upper level of the eyes. These characteristics have been observed in *C.*

prehensilis (Voss 2011; Racero-Casarrubia et al. 2016), therefore, this record is tentatively assigned to this species.

New localities and distribution update: We found one record MHNUCa (uncatalogued; skeleton and quills) from San Juan de Nepomuceno, Bolívar (10°05′50.9″N - 75°07′02.4″W; 226 m), which fills the gap on the presence of *C. prehensilis* in this department of the Caribbean region of Colombia. Based on photographs, we found confirmed records from two departments: Antioquia, corregimiento of Puerto Claver, El Bagre (7°36′17″N - 74°48′31″W; ~50 m), and Casanare from the municipality of Paz de Ariporo, vereda Colombina (06º12′17.01″N - 71º21′30.98″W; ~150 m), and from the municipality of Villanueva, vereda La Camarga - Leche Miel (4°36′19.3″N - 72°51′41.7″W; 420 m). External characters including large size, tricolored spines (whitish base) and last third of the naked tail (without spines) allow the assignment of the photographs to *C. prehensilis*. Additionally, a photography record from the Department of Cesar, “La Loma” (9°40'40.56"N - 73°32'40.19"W; ~46 m), confirms the presence of the species in this zone of Colombia.

Genetics: The specimen sequenced (IAvH 6787, from Toledo, Norte de Santander) appears as the sister taxon of 17 more sequences downloaded from GenBank, which are unambiguously assignable to *C. prehensilis* based on literature (Bonvicino et al. 2012; Voss et al. 2013). All these sequences conform a monophyletic group with strong support in our Bayesian cyt-b tree, confirming the taxonomic identity of IAvH 6786 as *C. prehensilis* (Fig. 4). Our phylogenetic analysis also provides a better supported sister relationship between *C. prehensilis* and a clade formed by *C. mexicanus*, *C. rufescens* and *C. quichua* (Fig. 4). The cyt-b sequence (entire coding region – 1140 bp) from IAvH 6786 constitutes the third molecular record for the species recovered from Colombian specimens. The mean genetic distances between this sequence and the other *C. prehensilis* sequences ranges from 0% (Valledupar, Cesar, Colombia), to 0.7% (Acre, Brazil). In addition, mean genetic distances between *C. prehensilis* and other *Coendou* species range from 7.3% with *C. mexicanus*, to 12.5% with *C. speratus*.

Discussion

Coendou prehensilis is the species of porcupine with the widest geographical distribution in Colombia (Fig. 1; Appendix). Based on our distribution update, the species has been registered in 16 continental departments, what corresponds to seven biogeographical provinces, and its presence is expected in the departments of Arauca, Cauca, Nariño, Huila, Santander and Vaupés. This wide distribution can be explained because the species is generalist, with wide home ranges, as well as tolerance to different types of ecosystems and elevational differences (Voss 2015). In other countries such as Brazil, it is also considered as one of the porcupines with a large distribution (de Freitas et al. 2013).

Previously, Voss (2015) and Ramírez-Chaves et al. (2016) suggested the presence of the *C. prehensilis* in the Colombian Orinoquía and the Ecuadorian, Brazilian, Peruvian and Venezuelan Amazon. Therefore, our records provide enough evidence to confirm its presence in the Colombian Amazon (Fig. 1). For other localities in the Colombian Amazon where the presence of *C. prehensilis* had been suggested, additional evidence is required. For example, Negret et al. (2015) performed an anecdotal record of *C. prehensilis* in the National Park Alto Fragua Indi-Wasi, which is located in the limits of the Department of Caquetá, but provide no any additional evidence about the presence of the species.

Additionally, our review of specimens from other localities allowed us to find some inconsistences on the known distribution of the species. For example, for the North Andean Province, there is only one record from the Magdalena river basin in the Department of Cundinamarca, based on a single specimen (ICN 443 skin and skull). This record is problematic because although the skull belongs to *C. prehensilis* the skin corresponds to *C. rufescens*, so the presence of *C. prehensilis* in this area needs more evidence and the record should be considered doubtful at this time.

As defined by cyt-b, *C. prehensilis* (sensu lato) comprises a genetically uniform species with nearly identical sequences scattered throughout its distributional range. Excluding an unusual divergent sequence from eastern Brazil (obtained from the neotype of *C. prehensilis*; Leite et al. 2011), the mean intraspecific distance is 0.5%, a value that is within the range of previously reported intraspecific variation in *Coendou* and other rodents (Bradley & Baker 2001; Voss et al. 2013). The small amount of genetic differentiation between our cyt-b sequence (IAvH 6786) and the two-other *C. prehensilis* sequences from Colombia available in GenBank (KC463876.1, KC463877.1), both recovered from specimens collected in the 1940´s at the same locality (Cesar, Valledupar; 10°29′N, 73°15′W; Voss et al. 2013), and identified as *C. sanctaemartae* by Alberico et al. (1999) provides further evidence on the assignation of *C. sanctaemartae* as a synonym of *C. prehensilis* (sensu lato), as also suspected on basis to morphology (Voss 2011; Ramírez-Chaves et al. 2016). All this shows that morphological and molecular data are essential to resolve basic aspects of the taxonomy and geographical distribution of neotropical porcupines, in this case, *C. sanctaemartae.* The latter was longer considered an endemic taxon from Colombia (Alberico et al. 1999; Solari et al. 2013), with probable presence in the lowlands of the Serranía de Perijá in both Colombia and Venezuela (Alberico et al. 1999), and Maracay, Venezuela (Ramírez-Chaves 2014).

Particularly in Colombia, the molecular characterization of porcupines remains incipient and there are only cyt-b sequences in GenBank from four of the seven species reported (Ramírez-Chaves et al. 2016). In this sense, the scarcity of molecular data of the genus is in part due to the lack of recent collections of all species. Furthermore, records of porcupines based on observations, road-killed individuals (de Freitas et al. 2013), captivity (Racero-Casarrubia et al. 2016), and presence of spines in the habitat or in carnivore feces (do Prado et al. 2008), are becoming useful tools to understand the current distribution of this poorly known group. From our observations, we consider that this type of direct and indirect evidence can contribute to clarify different aspects of the biology of the species of the genus at the national level.

Finally, in spite of the recent advances contributing to clarify aspects on the geographical distribution and morphological characteristics of *Coendou* species in Colombia, porcupines are still a poorly known mammalian group, both at national and Neotropical level (Voss 2011). For this reason, it is necessary to generate new information on their distribution, ecology, genetics, systematics, taxonomy among other topics. Even so, the threat to the porcupines is evident, being documented as the main ones the loss of habitat, illegal traffic, road-kills, and hunting for consumption (de Freitas et al. 2013; Racero-Casarrubia et al. 2016). In Colombia, for *C. prehensilis* specifically, has been documented illegal traffic and use as a pet (Racero-Casarrubia et al. 2016), activity that according to our photographic records is recurrent in the Amazon region. In summary, this work provided key information to corroborate the presence of the species in localities where the records are considered as questionable and allows an update of the distribution of the species at the national level.

Acknowledgements

We especially thank Luiz H. Varzinczak provided useful comments on an early version of the manuscript. Rances Caicedo for the photography of the individual from Puerto Alegría (Amazonas); Néstor Javier Roncancio Duque for the photography of the individual from Leticia (Amazonas); Juan Fernando Acevedo for sharing the video of the individual from the vicinity of the biological station “El Zafire” in the Colombian Amazon Trapeze; Wilber Ruíz for the photography of the individual from Paz de Ariporo (vereda “La Colombina”); María Meza from Universidad Industrial de Santander for the record and photography of the individual from Villanueva, Casanare; and Laura Vélez for the photograph of the individual from Bagre in Antioquia (corregimiento of Puerto Claver), which contributes to the updating of the distribution of the species in Colombia. Darwin Morales and Catalina Cárdenas provided photographs of ICN 21151. Fernando Sarmiento Parra, Cristian Cruz (MLS), Hugo López (ICN), Jairo Pérez-Torres (PUJ), for allow the review of specimens under their care. Abelardo Rodríguez for the collaboration with the information of the specimen housed in the MUD. Miguel Leonardo Martínez, for the collaboration during the visits to MLS. MMT-M thanks CAPES-DS for funding. HERC thanks to IAvH (Andrés M. Cuervo and María López Rodríguez) for access to the tissues analyzed in this document, and to Rufford Small Grants (Grant 23710-1) for support.

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Appendix.

Specimens reviewed (n=23), photographs and videos (n=9), and localities (n=32) used to update the distribution of *C. prehensilis* in Colombia. Abbreviations that do not appear in the text: AMNH: American Museum of Natural History, New York; FMNH: Field Museum of Natural History, Chicago; USNM: Smithsonian Institution National Museum of Natural History, Washington; UV: Universidad del Valle, Cali; ZSM: Zoologische Staatssammlung München, Munich.

Amazonas: Leticia, headquarters of the Universidad Nacional de Colombia (04°11′37″S, 69°56′27″W; 96 m.: photograph). El Zafire, 3.5 km of the biological station “El Zafire” (03°56′48″S, 69°53′11″W; 80 m.: video). Puerto Alegría (01°00′20″S, 74°00′54″W; 120 m.: photograph). **Antioquia**: El Bagre, Corregimiento de Puerto Claver (07°36′17″N, 74°48′31″W; 50 m.: photograph). **Atlántico**: Barranquilla (10º57′50″N, 74º47′49″W; 60 m.: ZSM 1956/199, 1957/167, 1957/187, 1958/9, 1958/10, 1958/20, 1958/76). **Bolivar**: Caldas, San Juan de Nepomuceno (10°05′50.9″N, 75°07′02.4″W; 226 m.: MHNUCa uncatalogued). **Boyacá**: Pajarito; Vereda Corinto (5°17′35″N, 72°42′11″W; 793 m.: ICN 3033). **Casanare**: Paz de Ariporo, Vereda La Colombina (06º12′17.01″N, 71º21′30.98″W; 149 m.: photograph). Villanueva (04º36′19.3″N, 72º51′41.7″W; 420 m.: photograph) **Caquetá**: Belén de los Andaquíes, road to the Eco Tourist Reserve “El Horeb” (01°24′37.20″N, 75°53′55.37″W; 320 m.: photograph). Florencia (01°36′51″N, 75°36′42″W; 242 m.: MLS 1093). Florencia, El Caraño, km 20 to Neiva (01°43′54.07″N, 75°40′39.93″W; 242 m.: ICN 23137). San José del Fragua, PNN Alto Fragua Indi-Wasi (01°33′45″N, 75°58′20″W; 367 m.: anecdotal record in Negret et al. 2015). **Cesár**: La Loma (09º40′40.56″N, 73º32′40.19″W; 46 m.: photograph). La Jagua de Ibirico, Corregimiento La Victoria, Vereda El Zumbador (09º36′19″N, 73º13′36″W; 220 m.: ICN 18567, 18568). Valledupar, Villanueva, Sierra Negra (09º35′09″N, 73º5′60″W; 220 m.: USNM 281897, 281898, 281901–281906, 281908, 281909, 281912, 281914). **Córdoba:** Monteria (08°34′24.65″N, 75°41′54.83″W; 49 m.: record in Racero-Casarrubia et al. 2016). **Guaviare:** San José del Guaviare, close to Laguna La María (02º31′42.26″N, 72º41′27.38″W; 210 m.: photograph). **Magdalena:** Bonda (11º14′05″N, 74º07′01″W; 60 m.: AMNH 15459, 15460, 23471–23473). Santa Marta, Minca, Farm "El Recuerdo" (11°08'32"N, 74°07'07"W; 636 m.: ICN Uncatalogued). **Meta:** Cubarral, Vereda Aguas Claras (03º48′37″N, 73º52′35″W; 860 m.: ICN 14932). Los Micos (03°18′40″N, 73°54′17″W; 400 m.: FMNH 87897). Villavicencio (04°08′33″N, 73°37′46″W; 460 m.: AMNH 73680, 136311; MLS 246; Estación Roberto Franco ICN 1419; AMNH 73680, 136311). San Martín, vereda La Castañeda, Finca Arrayanes (03°41′N, 73°41′W; 405 m.: MPUJ-MAMM:2163, skin). **Norte de Santander:** San Cayetano, vereda Tabiro, Farm Hortencia (07º51′00″N, 72º36′59″W; 300 m.: ICN 21448). Toledo, Sector Ríonegro, Parque Nacional Natural Tama (7°14′36″N, 72°13′19″W; 600 m.: IAvH 6786). **Putumayo:** Mocoa (01°14′32″N, 76°30′28″W; 604 m.: ICN 21151). **Sucre:** Tolú (09º31′44″N, 75º34′04″W; 10 m.: IAvH 4097). **Vichada:** Puerto Carreño (06º12′25″N, 67º29′01″W; 90 m.: UV 8834). Parque Nacional Natural Tuparro (05º15′23″N, 68º25′35″W; 100 m.: IAvH 3037, 3072). Reserva Natural Bojonawi (6° 6'8.10"N, 67°29'26.30"W; 52 m.: MUD 566).

Doubios records: Cundinamarca, Fusagasugá, 4 km on the road to La Aguadita (04º23′30″N, 74º19′22″W; 1975 m.: ICN 443).

Table 1. Cranial measurements of a specimen of *C. prehensilis* (MLS 1093) from the Colombian Amazon. Measurements of specimens from other localities of Colombia were obtained from Ramírez-Chaves et al. (2016) and the revision of copies of the Museo de La Salle (MLS 246) and Instituto de Ciencias Naturales (ICN). Colombia (Biogeographic Provinces): AM, Amazonia; OR, Orinoco; CA, Peri-Caribbean arid belt; GU, Guyana; NA, North Andean. The values indicate the average, interval (in parentheses) and the number of individuals. No specimens from the Magdalena region of the Chocó-Magdalena Province are available for cranial comparisons.

Measurements	**Colombia**				
	AM	**OR**	**CA**	**NA**	**GU**
CIL	82.66 (79.82-85.5) 2	92.92 (92.03-93.82) 2	82.02 (75.08-87.1) 9	86.30 1	-
LD	21.19 (20.07-22.3) 2	25.22 (23.25-27.2) 2	21.028 (18.16-24.7) 9	21.66 (19.83-23.5) 2	27.2 1
MTR	19.59 (19.17-20) 2	20.55 (20.07-21.2) 3	19.11 (17.91-20.85) 9	18.44 (19.1-20.39) 3	21.2 1
LM	14.84 (14.47-15.2) 2	15.49 (15.4-15.92) 3	14.17 (12.76-15.27) 9	13.99 (13.2-14.79) 2	15.4 1
BP4	4.72 (4.03-5.4) 2	5.70 (5.7-5.71) 2	5.49 (4.63-6.7) 10	5.19 (4.9-5.77) 3	5.7 1
BM1	5.12 (4.63-5.6) 2	5.65 (5.5-5.81) 2	5.39 (4.79-5.74) 10	5.54 (5.2-5.89) 2	5.5 1
APB	7.77 (7.74-7.79) 2	6.87 (6.85-6.9) 2	6.37 (4.6-7.8) 10	6.15 (5.55-6.3) 2	6.9 1
PPB	10.39 (9.18-11.6) 2	10.32 (10.21-10.43) 2	8.43 (8.03-9.14) 9	8.74 (8.47-9) 3	-
PZB	51.87 (50.5-	56.62 (54.07-	50.05 (46.74-	52.39 (50.92-	57.9 1

	53.23) 2	57.9) 3	53.16) 8	53.7) 3	
HIF	12.89 (10.32-15.45) 2	15.33 (13.01-16.9) 3	12.57 (8.65-14.68) 10	13.36 (11.74-15.63) 3	16.9 1
ZL	32.95 (31.99-33.9) 2	37.44 (35.5-38.87) 3	32.56 (31.06-35.69) 9	32.89 (33.87-31) 3	35.5 1
LN	28.98 1	34.42 1	30.98 (27.63-34.94) 5	-	-
BNA	20.93 1	24.64 (22.94-26.6) 3	18.35 (15.25-20.53) 9	20.23 (19.8-20.66) 2	26.6 1
BB	38.79 (38.1-39.47) 2	42.88 (39.33-48.5) 3	36.13 (34.29-38.1) 10	35.46 (35.42-35.5) 2	48.5 1
DI	4.24 1	5.11 1	3.93 (3.07-4.38) 9	4.67 (3.8-5.55) 2	-
BIT	5.94 1	6.79 1	8.42 (6.8-10.73) 9	7.88 (7.77-8) 2	-

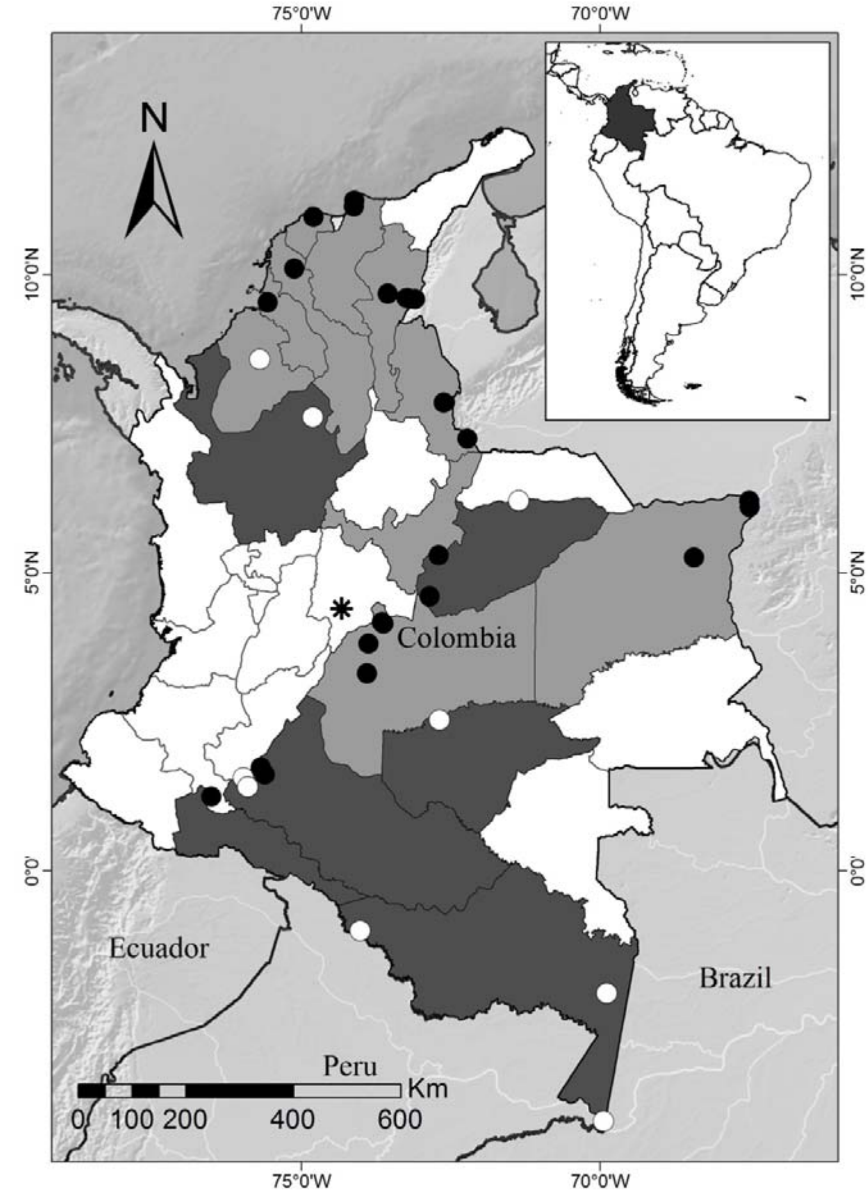

Figure 1: Distribution of *Coendou prehensilis* in Colombia. Light gray: departments with previous records of the species. Dark gray: departments where the species is confirmed based on our new records. White: departments without records of the species. Black spots: records based on voucher specimens. White spots: photographic or video records. Asterisk: dubious record.

Figure 2: Skull (top) and skin (bottom) of *Coendou prehensilis* (MLS 1093) from the Colombian Amazon. Top: dorsal and ventral view of the skull; Middle: lateral view of skull and mandible in dorsal view. Bottom: details of the skin where bi and tri-colored spines can be observed. Maximum skull length: 85.5 mm.

Figure 3: Details of bi and tri-colored spines of *Coendou prehensilis* (ICN 23137) from the Colombian Amazon region.

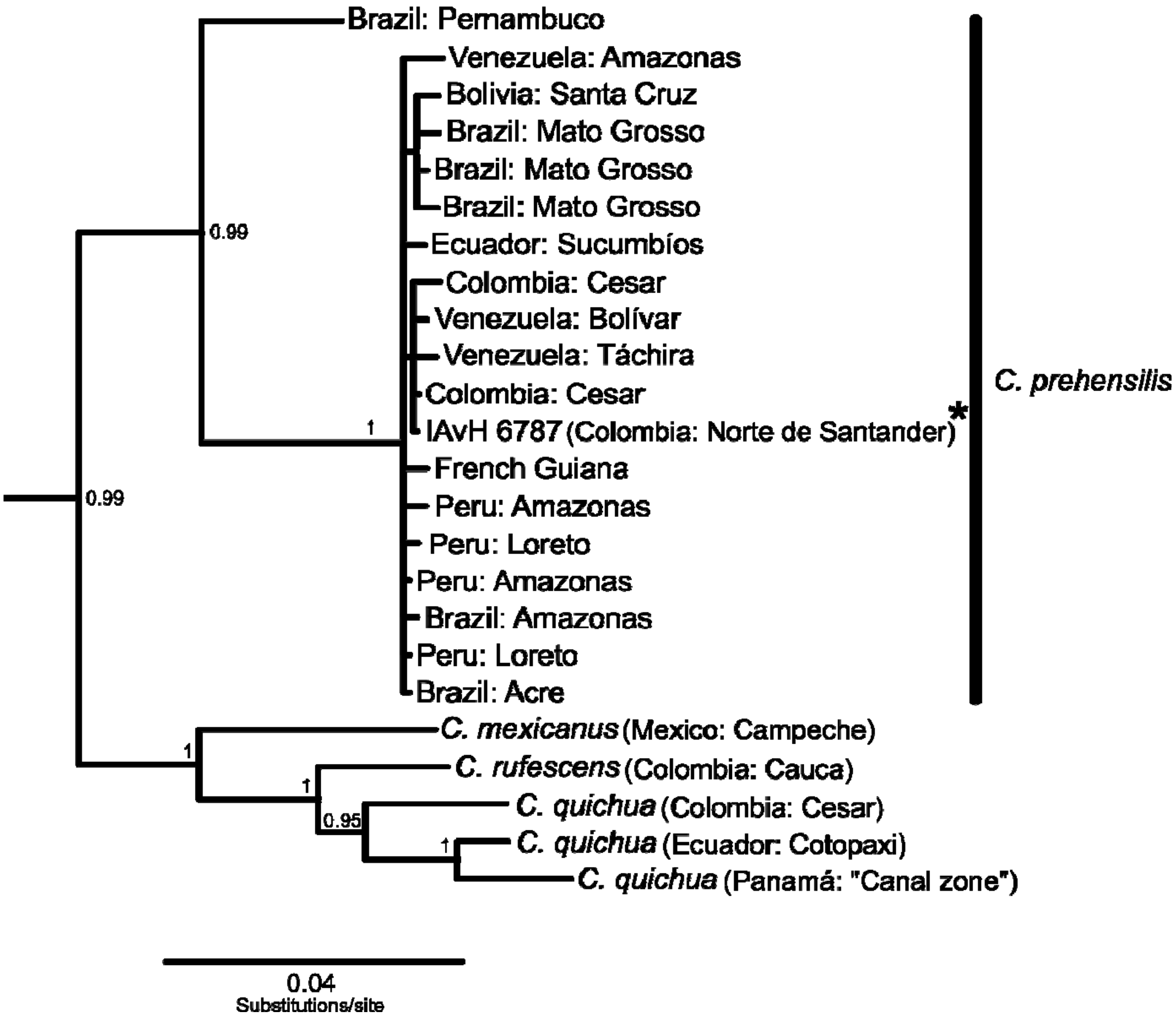

Figure 4: Bayesian cyt-b tree of *Coendou prehensilis (sensu lato)* and sister taxa. Specimens are identified by country of origin and next largest political unit. The new molecular record for the species presented here is highlighted by an asterisk. Nodal support values are posterior probabilities.

V CONCLUSIONS AND FUTURE RESEARCH

Coendou represents a charismatic group with wide distribution in the Neotropics. However, as shown in this dissertation, there are still gaps in information either for common species (i.e. *C. prehensilis*) or rare ones (i.e. *C. vestitus*). Several questions remain open, as for example the reasons behind the current distribution for widely or restricted species, that could be evaluated in a near future, using as a baseline, the information provided in this dissertation.

In particular, *C. vestitus* is the species with the most limited distribution, with only few records and three validated localties, all in the Eastern Cordillera of Colombia. According to the distribution model shown in Chapter I, this species has a potential distribution in the Central Andes of Colombia, however, field work should be performed in that area to validate the distribution hypothesis. In addition, *C. vestitus* has the highest level of rarity, due to the reduced distribution area and that only inhabits one type. Additionally, in Chapter I, genetic data helps to clarify the phylogenetic position of this species, considering that this kind of information is scarse. With all this information I suggest the transfer of the threathen category DD (Deficient Data) to EN (Endangered).

In contrast, *C. prehensilis* is the most widely distributed species in South America, however, little is known even for basic aspects as its regional distribution. For example, in Colombia, there was no evidence of its presence in the Amazon region (see Chapter II), although it was known from this region in the Amazon of Brasil, Ecuador, and Peru. After a carefull review of literature, photographs and voucher specimens, its distribution was updated, and the species was confirmed in that region (Chapter II), thus covering seven of the Colombia's biogeographic provinces. An additional result shows that the only known record from the the inter-

Andean region of Magdalena river Basin in central Colombia (Department of Cundinamarca) is doubtful and should not be longer included in the distribution of the species. Furthemore, the genetic information in Chapter II, provides additional evidence in favour of considering *C. sanctaemartae* (a taxon suggested as endemic of Northern Colombia) as a junior synonym of *C. prehensilis* (sensu lato). Despite that, a new genetic characterization of the species is needed to clarify the taxonomic problems that are common in the group. In conclussion, relative common species lack basic information as distribution, ecology and taxonomy.

Finally, this dissertation provides key information that contributes in the knowledge of the genus *Coendou* in the Neotropics, especially in Colombia, and can be used to clarify aspects about its geographical distribution and morphological characters of the species evaluated and related taxa. Nevertheless, additional work is needed in topics as distribution, ecology, genetics, systematics, taxonomy among others, at national and Neotropical level. Particularly, the relation between morphological characters and the distribution ranges of common and rare species is a topic that is expected to be evaluated using the information obtained from this dissertation. In addition, integrative research including different aspects as the state of knowledge, genetics, conservation, and ecology should be evaluated for all the species of the genus.

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