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On the distribution of the Brazilian porcupine *Coendou prehensilis* (Erethizontidae) in Colombia

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 Llanos 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 the literature, the presence of the species in the Colombian Amazon is confirmed, and its distribution in the country updated. Overall, we found 36 records of *C. prehensilis* in Colombia, of which seven correspond to the Colombian Amazon (four photographic records and three specimens). A genetic analysis based on cytochrome-b suggests that this species is genetically uniform throughout its distributional range. These new records make *C. prehensilis* the most widespread species of the genus among natural regions and biogeographic provinces of Colombia. Other species are restricted to one or two provinces.

Introduction

The genus *Coendou* Lacépède, 1799 is distributed in tropical and subtropical forests from Mexico to Uruguay, and comprises between 13 and 15 species (Voss 2015, Barthelmess 2016). Among them, the Brazilian porcupine *Coendou prehensilis* (Linnaeus, 1758) presents the widest distribution. The species is known to occur 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, *Coendou 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, and the presence in some national provinces is still doubtful. Furthermore, populations in the Caribbean region of the country have been considered as a distinct taxon (*Coendou sanctaemartae* J. A. Allen,

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1904; see Alberico et al. 2000, Solari et al. 2013), and some melanistic individuals were misidentified as *Coendou bicolor* (Tschudi, 1844) (Ramírez-Chaves et al. 2016). Here, we confirm the presence of *C. prehensilis* in the Colombian Amazon, provide a new cytochrome-b sequence of one individual from northern Colombia, and an update of its distribution in the country. We also discuss the validity of *C. sanctaemartae*.

Materials and methods

We reviewed specimens deposited at the 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 (MHN-UCa), Manizales; and Colección de Mamíferos del Museo Javeriano de Historia Natural "Lorenzo Uribe Uribe" (MPUJ), Bogotá, not included in previous reviews in Colombia (e.g. Alberico et al. 2000, Ramírez-Chaves et al. 2016). To corroborate the identification of the reviewed specimens, we used cranial and external characters available in the literature (e.g. Voss 2011, 2015, Ramírez-Chaves et al. 2016). For this, the following cranial measurements (in millimeters) were taken from adult specimens: condylo-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 four photographic records from the Colombian Amazon, two from the Orinoco, and one each from the Andean and Caribbean regions. Also, we reviewed a video of a specimen recorded as *Coendou melanurus* (Wagner, 1842) in the literature (Acevedo-Quintero and 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 made a genetic characterization of one specimen housed at the Colección de Mamíferos of the Instituto Alexander von Humboldt – IAvH (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 *Coendou prehensilis* and *Coendou*

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 Fisher Scientific, Waltham, MA, USA), following the manufacturer's recommendations. We amplified the entire mitochondrial cytochrome-b gene (*cyt-b*) in two overlapping fragments of ~700 base pair (bp) using the primers MVZ05 paired with PorcCytb676R, and PorcCytb565F paired with UMMZ04 (Voss et al. 2013). Polymerase chain reaction (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). 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 dNTPs, 0.2 μM of each primer and 1.25 u/μl of DreamTaq DNA polymerase (Thermo Scientific, Waltham, MA, USA). Sequencing of purified PCR products was performed in both directions with the amplification primers on an ABI 3500 sequencer (Applied Biosystems, Waltham, MA, USA) at the "Servicio de Secuenciación y Análisis Molecular SSiGMol" at the Universidad Nacional de Colombia, Bogotá, Colombia. We used Geneious R11 (Biomatters Limited, Auckland, New Zealand) 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 Multiple Sequence Comparison by Log-Expectation (MUSCLE) algorithm as implemented in Geneious R11 (Biomatters Limited, Auckland, New Zealand). We analyzed the aligned sequence data using Bayesian inference (BI) in Mr Bayes 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 it was implemented in the running of two independent Markov chain Monte Carlo (MCMC) analyses for 2×10^7 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, the 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 Molecular evolutionary genetics

analysis (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 and Baker 2001) and specifically for porcupines (Voss et al. 2013).

Results and discussion

Distribution

Coendou prehensilis is present in 36 localities from 24 municipalities 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 (Figure 1).

We confirmed the presence of *Coendou prehensilis* in the Colombian Amazon based on one female *C. prehensilis* preserved as skin and skull (MLS 1093), collected in 1950, municipality of Florencia (1°36′51″N – 75°36′42″W; ~242 m), and on one specimen found dead on April 8 2015 (ICN 23137) in El Caraño, km 20 road to Florencia-Neiva (1°43′54.07″N – 75°40′39.93″W; ~242 m), both in the department of Caquetá. Both specimens exhibit the diagnostic
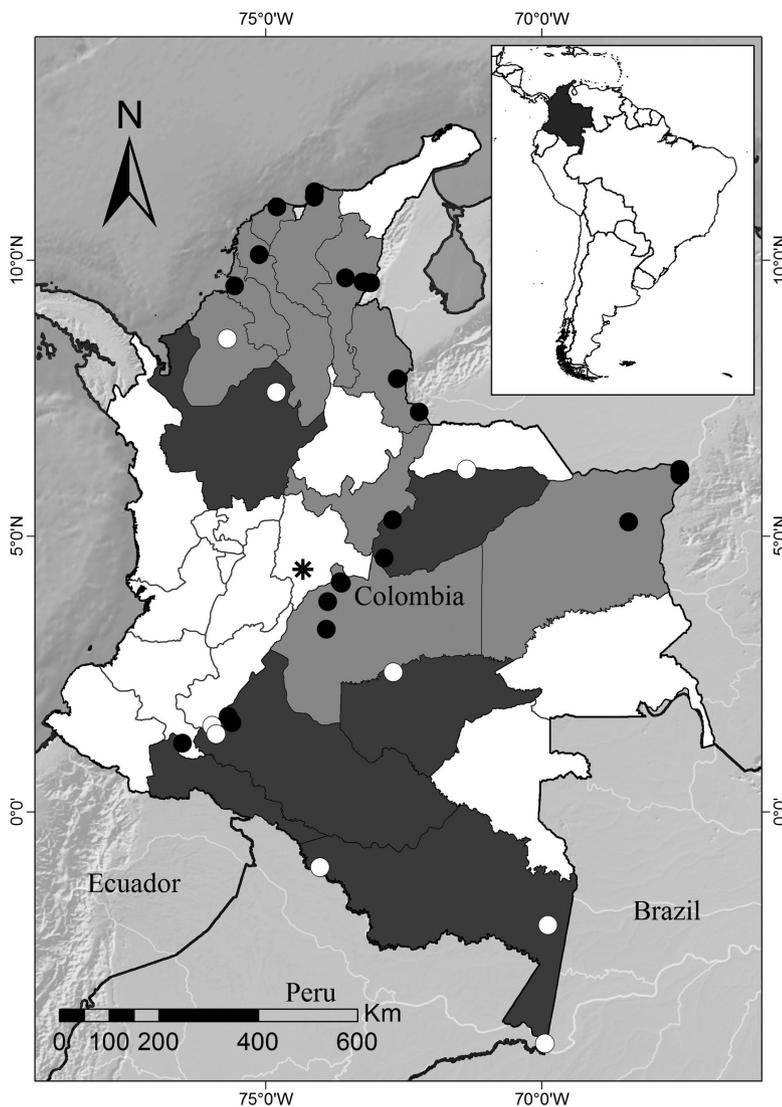

Figure 1: Distribution of *Coendou prehensilis* in Colombia.
Light gray: departments with previous records. Dark gray: departments where the species is confirmed based on our new records. White: departments without records. Black spots: records based on vouchers. White spots: photographic or video records.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

morphological characteristics of the species (Voss 2011, 2015; Figures 2 and 3). 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 (Figure 3); cranially, the frontal sinuses are inflated, the nasal aperture is wide and the upper incisors are distinctively procumbent (Leite et al. 2011, Voss 2011, 2015, de Freitas et al. 2013). The cranial measurements of MLS 1093 and ICN 23137 match those recorded for other specimens from Colombia (Table 1; Ramírez-Chaves et al. 2016). One skull from Natural Reserve "Bojonawi", Vichada (MUD 566; 6°6′8.10″N – 67°29′26.30″W; ~49 m), also confirms the presence of the species in the limits of the Orinoco and Amazon basins, whereas one specimen (MHN-UCa 1604, skeleton and quills) from San Juan de Nepomuceno, Bolívar (10°05′50.9″N – 75°07′02.4″W; 226 m), fills the gap on the presence in this department of the Caribbean region.

In addition, we examined 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 the soft hair that is characteristic of immature individuals (Voss and da Silva 2001). Although the identification of ICN 21151 is complex because it lacks diagnostic characters, it is tentatively assigned to *Coendou 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.

From photographs (Figure 4), the species is recorded in four localities from the Colombian Amazon region in the departments of Amazonas, Caquetá and Guaviare (Supplementary Appendix 1). We also reviewed the photographic records (Figure 4) that confirm the presence of the species in the departments of Antioquia, Casanare and Cesar (Supplementary Appendix 1). 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 *Coendou prehensilis*.

Genetics

The specimen sequenced (IAvH 6787, from Toledo, Norte de Santander) appears clustered with 17 more sequences downloaded from GenBank, which are unambiguously assignable to *Coendou prehensilis* based on the literature (Bonvicino et al. 2002, Voss et al. 2013). All these
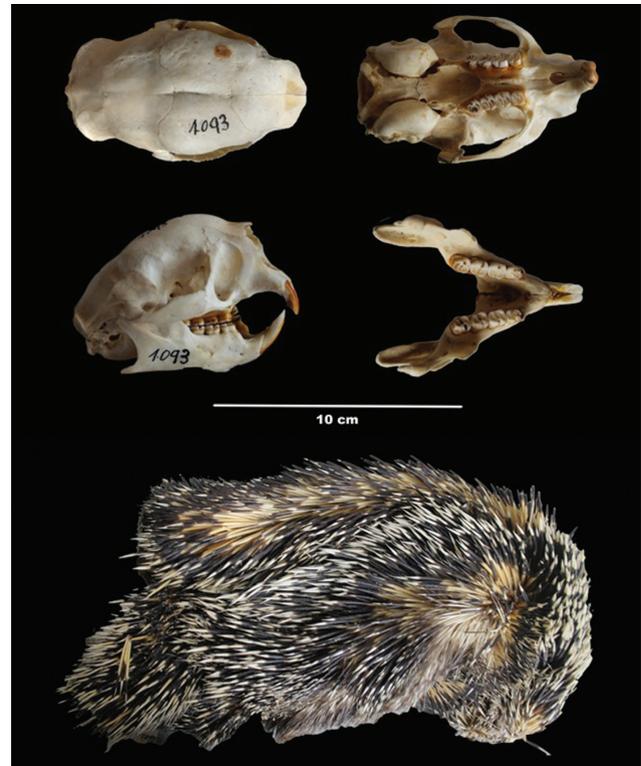
Figure 2: Skull (top) and skin (bottom) of *Coendou prehensilis* (MLS 1093) from the Colombian Amazon.
Top: dorsal and ventral view of the skull; Middle: lateral view of skull and mandible in dorsal view. Bottom: details of the skin where bi and tri-colored spines can be observed. Maximum skull length: 85.5 mm.

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

sequences conform a monophyletic group with strong support in our Bayesian *cyt-b* tree, confirming the taxonomic identity of IAvH 6786 as *C. prehensilis* (Figure 5).

Table 1: Measurements of 19 specimens of *C. prehensilis* from the Colombian Amazon and other provinces of Colombia (from Ramírez-Chaves et al. 2016).

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	–
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
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
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
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
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
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
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 (50.5–53.23) 2	56.62 (54.07–57.9) 3	50.05 (46.74–53.16) 8	52.39 (50.92–53.7) 3	57.9
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
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
LN	28.98	34.42 1	30.98 (27.63–34.94) 5	–	–
BNA	20.93	24.64 (22.94–26.6) 3	18.35 (15.25–20.53) 9	20.23 (19.8–20.66) 2	26.6
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
DI	4.24	5.11	3.93 (3.07–4.38) 9	4.67 (3.8–5.55) 2	–
BIT	5.94	6.79	8.42 (6.8–10.73) 9	7.88 (7.77–8) 2	–

Biogeographic provinces: AM, Amazonia; OR, Orinoco; CA, Peri-Caribbean arid belt; GU, Guyana; NA, North Andean. No specimens from the Magdalena region of the Chocó-Magdalena Province were available for cranial comparisons. Average (interval in parentheses) and the number of individuals.

Our phylogenetic analysis also provides a better-supported sister relationship between *C. prehensilis* and a clade conformed by *Coendou mexicanus* Kerr, 1792, *Coendou rufescens* (Gray, 1865) and *Coendou quichua* Thomas, 1899 (Figure 5). 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, the mean genetic distances between *C. prehensilis* and other *Coendou* species range from 7.3% with *C. mexicanus*, to 12.5% with *Coendou speratus* Mendes Pontes, Gadelha, Melo, de Sá, Loss, Caldara Junior, Costa, and Leite, 2013.

Discussion

Coendou prehensilis is the species of porcupine with wider geographical distribution in Colombia (Figure 1; Supplementary Appendix 1). It has been registered in 16 continental departments, 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 large 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 a widespread species (de Freitas et al. 2013).

Previously, the presence of the *Coendou prehensilis* in the Colombian Orinoquía and the Ecuadorian, Brazilian, Peruvian and Venezuelan Amazon was suggested (Voss 2015, Ramírez-Chaves et al. 2016). Therefore, our records provide enough evidence to confirm its presence in the Colombian Amazon (Figure 1). For other localities in the Colombian Amazon where the presence of *C. prehensilis* had been suggested, additional evidence is required. For example, an anecdotal record of *C. prehensilis* in the National Park Alto Fragua Indi-Wasi, Caquetá (Negret et al. 2015), provided no evidence about the species presence. Another literature record from the Colombian Amazon identified as *Coendou melanurus* (Acevedo-Quintero and Zamora-Abrego 2016) is based on a video in which a large individual with only one type of spines, and the anterior part of the nostrils located above the upper level of the eyes is observed, is tentatively assigned here to *C. prehensilis*.

Additionally, our review of specimens from other localities allowed us to find some inconsistences in the known distribution of the species. For example, for the inter-Andean valley of the Magdalena River basin in 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

Figure 4: Additional records of *Coendou prehensilis* from Colombia.
(A) Amazonas, Leticia, headquarters of the Universidad Nacional de Colombia. (B) Amazonas, Puerto Alegría. (C) Antioquia, El Bagre, Corregimiento de Puerto Claver. (D) Casanare, Paz de Aripo019, Vereda La Colombina. (E) Casanare, Villanueva. (F) Cesar, La Loma.
(G) Guaviare, San José del Guaviare, close to Laguna La María. (Photographs: (A) Nestor Roncancio, (B) Rancés Caicedo, (C) Laura Vélez, (D) Wilber Ruíz, (E) María Meza, (F) Javier Colmenares, (G) Juan Pablo López.)

skull belongs to *Coendou prehensilis* the skin corresponds to *Coendou rufescens*, so the presence of *C. prehensilis* in this area needs more evidence and the record should be considered doubtful at this time.

In terms of *cyt-b*, *Coendou 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 and Baker 2001, Voss et al. 2013). The short 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 1940s at the same locality (Cesar, Valledupar; 10°29′N, 73°15′W;
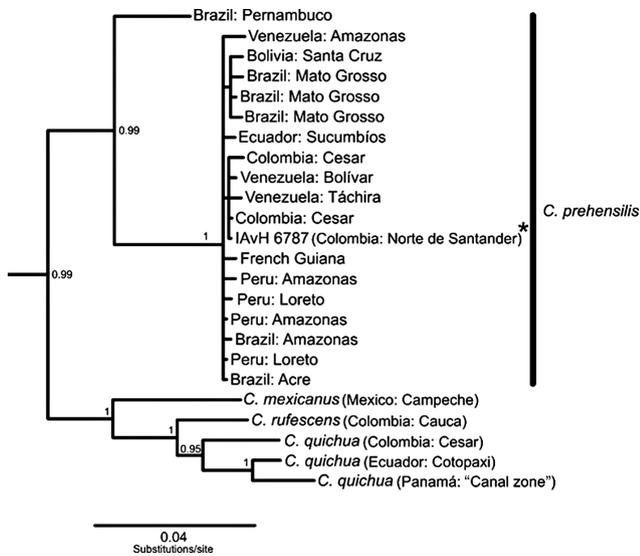
Figure 5: Bayesian *cyt-b* tree of *Coendou prehensilis* (*sensu lato*) and sister taxa.
Specimens are identified by country of origin and next largest political unit. The new molecular record for the species presented here is highlighted by an asterisk. Nodal support values are posterior probabilities.

Voss et al. 2013) and identified as *Coendou sanctaemartae* by Alberico et al. (2000), provides further evidence on the assignment of *C. sanctaemartae* as a synonym of *C. prehensilis* (*sensu lato*), as also suspected on the basis of morphology (Voss 2011, Ramírez-Chaves et al. 2016). All this shows that morphological and molecular data are essential to resolve the basic aspects of the taxonomy and geographical distribution of neotropical porcupines, in this case, of *C. sanctaemartae*, which was long considered a distinct endemic taxon (Alberico et al. 2000, Solari et al. 2013), but probably present in the lowlands of the Serranía de Perijá in both Colombia and Venezuela (Alberico et al. 2000) 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). The scarcity of molecular data of the genus is in part due to the lack of recent collections of all species. Furthermore, accumulating records of porcupines based on observations, road-killed individuals (de Freitas et al. 2013), captivity (Racero-Casarrubia et al. 2016), and the presence of spines in the habitat or in carnivore feces (do Prado et al. 2008), are becoming a useful tool to understand the current distribution of this poorly known group. We consider that this type of direct and indirect evidence can contribute to clarify different the aspects of the biology of the species of the genus at the national level.

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